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Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England

J. J. Hooker

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The lithostratigraphy of deposits laid down during the Bartonian in the Hampshire Basin is described. The new formal terms Barton Clay Formation and Becton Sand Formation are defined. The Elmore Formation is reduced to member rank within the Barton Clay Formation. A pattern of cyclic sedimentation within the Barton Clay Formation, Becton Sand Formation and part of the Boscombe Sands is recognized.

Fifty-three mammalian taxa of species group rank, represented mainly by teeth but also by some important cranial and postcranial elements, are described from the Creechbarrow Limestone and Barton Clay Formations. Of these, 12 are new: *Gesneropithex figularis*, *Nannopithex quaylei*, *Microchoerus wardi*, *M. creechbarrowensis*, *Europolemur collinsonae*, *Plesiarctomys curranti*, *Sciuroides rissonei*, *Suevosciurus authodon*, *Heterohyus morinionensis*, *Vulpavoides cooperi*, *Plagiolophus curtisi* and *Haplobunodon venatorum*. *Plagiolophus curtisi* is divided into two subspecies, the nominate one and *P. curtisi creechensis*. *Treposciurus helveticus* is here raised from subspecific rank and a new subspecies, *T. h. preecei*, is added. Some species formerly placed in *Anchomomys* (order Primates) are included in *Gesneropithex* (order Lipotyphla). The contents of the family Pseudosciuridae and of the genera *Cebochoerus* and *Acotherulum* are revised. Genus records from Creechbarrow are the earliest for *Treposciurus* and *Suevosciurus* and the latest for *Nannopithex*, *Europolemur* and *Vulpavoides*. Of the named taxa, 11 of the genera and all except three of the species are new records for the English Palaeogene.

Biostratigraphic correlation within the Bartonian of Europe, especially that by means of mammals, is discussed. Two mammalian concurrent range biozones, spanning the late Lutetian and Bartonian, are defined. Correlation from the non-marine to marine facies is attempted by integrating the mammal data with those from other organisms.

Tentative conclusions are drawn concerning depositional environments; mammalian palaeoecology is discussed for the Creechbarrow locality. Some aspects of palaeogeography are considered for the European Bartonian.

Introduction

Land mammals have long been known from Ludian deposits of the Hampshire Basin (e.g. Wood 1846) and have been the subject of some recent studies (e.g. Bosma 1974, Cray 1973, Insole 1972). They are much scarcer in the underlying marine Barton Clay and the discovery of

several specimens by amateur geologists at Barton Cliff was a matter of interest (Hooker 1972). However, the small number of specimens and the unlikelihood of any more coming to light seemed to preclude further studies. An independent investigation of the equivocally dated non-marine Creechbarrow Limestone, launched in 1975, led to the discovery of a rich mammalian fauna of Bartonian age (Hooker 1977*b*). The small number of mainland European Bartonian mammal sites makes this fauna important on a continental scale. The pioneers of Creechbarrow geology, Hudleston (1902*a*, 1902*b*, 1903) and Keeping (1910, 1912), made large excavations, but without undertaking any sieving of the sediment. In recent decades sieving has come to the fore as a field technique (e.g. Kühne 1969, McKenna 1962, Insole 1972), and the rich fauna described here was retrieved solely by this means.

It was decided to undertake a detailed taxonomic treatment of all the available English Bartonian mammals, which are known only from the Hampshire Basin. Some basic lithostratigraphic classification was found to be necessary for much of the sequence of strata, because of the mixed nature of earlier stratigraphic studies and the recent indiscriminate application of formal lithostratigraphic rank terms to non-lithostratigraphic or undefined units.

The presence of land mammals in the marine as well as the fresh-water facies of the Hampshire Basin suggested the possibility of biostratigraphic correlation across this otherwise difficult environmental boundary. A possible reconciliation of some of the discrepancies between current mammalian and marine invertebrate zonal and dating schemes in Europe was thus envisaged. A brief interpretation of the environments and mammalian palaeoecology and palaeobiogeography was also considered a useful corollary and to make the study as comprehensive as possible.

Materials and methods

Collecting

Collecting by the author and his colleagues was restricted to the Creechbarrow locality. Material from other localities was mainly the result of collecting by enthusiastic and competent amateur geologists.

The first attempt at excavation of the Creechbarrow Limestone at Creechbarrow was carried out on a Tertiary Research Group field meeting from 19–20 July 1975. Trench excavation was begun on the east side of the hill just below the summit, but had to be abandoned because of the amount of hillwash and talus, probably from old excavations. A second excavation (Hole 1) was opened higher and immediately east of the summit trigonometrical point. In this hole, below the soil layers, marl and rotted limestone were found and 27 kg were removed. This sample yielded the first remains of mammals since Keeping's work (1912). Hole 1 was widened and deepened on 2 August 1975 to become Hole 2 (subsequently considered together with Hole 1) and 282 kg of matrix were removed. Hole 3 was dug on 6–7 December 1975 and 840 kg were removed. More intensive excavation work funded by the British Museum (Natural History) (BM(NH)) was carried out from 30 May–4 June 1976 and resulted in the removal of 4190 kg of matrix from Holes 4 and 5. A further BM(NH) excavation from 28 July–12 August 1978 resulted in Holes 6 and 7, about 5700 kg being removed from Hole 6.

Matrix from Holes 1–5 was removed entire for laboratory processing. Most of that from Hole 6 was initially wet-sieved in a nearby flooded quarry, using an Alcon water pump and a stack of sieves ranging in mesh size from 10 mm to 0·5 mm. The concentrate was then transported back to the BM(NH). A map of the holes is shown in Text-fig. 4, p. 209.

The present report covers material recovered by complete processing of the marl matrix from Holes 1–3 and part of Hole 4 (bags 1–36); and initial coarse processing for larger, rarer species from the rest of Hole 4 and Holes 5–6. Matrix processed in the laboratory was first allowed to dry, weighed and allowed to break down in hot water before being sieved through 0·5 mm mesh size. The residue was dried and graded above and below 4 mm mesh. The dried fraction >4 mm was then sorted for fossils. The 0·5–4 mm fraction was treated with dilute acetic acid to remove the limestone fragments. The insoluble residue was washed of acid salts, dried and

graded above and below 1 mm mesh for greater ease of sorting. In a trial sample of the lower size fraction, nothing but a few bone fragments was found. Although all of this size fraction was retained for further concentration in the future, only that above 1 mm was sorted further for vertebrates and any other fossils that had survived the acid treatment. This fraction was found to be rich in mammals, at a concentration of about one tooth per kilogram of unprocessed matrix (dry weight). The inorganic insoluble residue in the acid-treated samples is mainly angular to subangular quartz sand.

All the material collected is in the Department of Palaeontology, British Museum (Natural History) and the distribution of numbered mammalian specimens per excavation hole is recorded below.

Holes 1/2: M35390–444, M35446–599, M36499, M36790–829, M36860.
Hole 3: M35600–6259, M36380–447, M36497–8, M36500.
Holes 4–5: M35445, M37090–571.
Hole 6: M37690–719.

Specimens already in museum collections are listed below. The BM(NH) cast number follows in brackets those in other museums, where relevant.

Barton: M11090, M12346, M26176, M26238, M26552–3, M26649, M29090–1, M34864–5.
Elmore: M36491, GM.978110-1 (M36493), GM.978110-2 (M36492), GM.978110–3 (M41977).
Hengistbury: IGS. GSM88617 (M31996).
Creechbarrow: SMC. C9968 and C9969 (M33501).

Curation of small teeth

The small teeth were all mounted on stainless steel entomological pins, inserted in corks, which were in turn inserted into flat-bottomed glass tubes. This allowed the register number to be written on an object (the cork) actually attached to each specimen, as well as on the glass tube, and should minimize long-term loss or muddling of specimens through study.

Measurements

The larger specimens were measured using an 8-inch Mitutoyo vernier caliper. Smaller specimens in the BM(NH) were measured using a calibrated micrometer eyepiece in a Nikon SMZ-10 binocular microscope; similarly calibrated micrometer eyepieces on a variety of binocular microscopes were used in other institutions.

The main tooth measurements are:

Maximum mesiodistal dimension (l);
Maximum buccolingual dimension (w);
Maximum buccolingual dimension of trigonid of lower molariform teeth (w_1);
Maximum buccolingual dimension of talonid of lower molariform teeth (w_2).

Thus in the case of incisors, e.g. of rodents, the mesiodistal dimension is in fact in a mediolateral direction and the buccolingual dimension in an anteroposterior direction. Where problems arise and/or exceptional parameters are used, this is discussed in the text. The standard deviation (s) and coefficient of variation (v) are calculated according to the methods of Simpson *et al.* (1960).

Photographic work

Pl. 35, fig. 1c (p. 434) was taken on a Leitz Ortholux II. Most of the other light macrographs were taken using a Zeiss Tessovar or a Leitz Aristophot. In nearly every case, the specimens were first coated with ammonium chloride to overcome the confusing effects of shine on tooth enamel and of preservational colour. The scanning electron micrographs (SEM) were taken using an ISI Stereoscan 60A. The specimens for scanning electron microscopy were cleaned with acetone, mounted on aluminium stubs using Durofix and photographed at 2 kv without coating. Absence of coating and use of Durofix as a mounting medium meant that the specimens could be easily returned to their normal storage without the tedious task of removing the coating. Teeth are figured as from the left side, i.e. figures of right teeth are shown reversed in nearly every case.

Taxonomic procedure

For each taxon in the systematic section (pp. 212–415), except where identification is only at a high taxonomic level, a diagnosis (new or emended) or a reference to the most recent diagnosis is given.

Synonymy lists for genera are not intended to be comprehensive but to give a range of the names that have been applied. Those for species refer mainly to the British material under discussion. Historical accounts of wider synonymy are given where relevant. Procedure and terminology follows Matthews (1973).

Where information from the English material has allowed clarification or changes in supra-specific groupings, either a stratophenetic (e.g. *Suevosciurus*) or a cladistic (e.g. Microchoerinae) approach has been employed. The choice was dependent on the nature of the available data (see Fortey & Jefferies 1982).

The importance of size differences in cheek teeth of mammals for distinction at species level is recognized (see Gingerich 1974, 1976*a*). High coefficients of variation (i.e. *c.*8 or more) for mainly length measurements of preultimate molars with or without polymodality of the normal curve is taken to indicate more than one species. Whilst it is always impossible with fossils to be completely certain, if large numbers of specimens produce a normal curve with a low coefficient of variation and continuous range of morphological variation, it is highly probable that one is dealing with a biospecies.

If the species concept is a difficult one, the problems of relating assemblages (especially ones in close stratigraphic succession) to named species, from which they differ only slightly, or of deciding on erection of subspecies, are almost insoluble within our present system of taxonomy. A general principle has been followed that a subspecific name may be used if the difference (either morphological or size) is noticeable but less than is found between closely related species from one locality, belonging to the same or a related genus. In cases of doubt, the specific prefix 'aff.' has been used, 'cf.' being retained for uncertainty of identification on account of incompleteness.

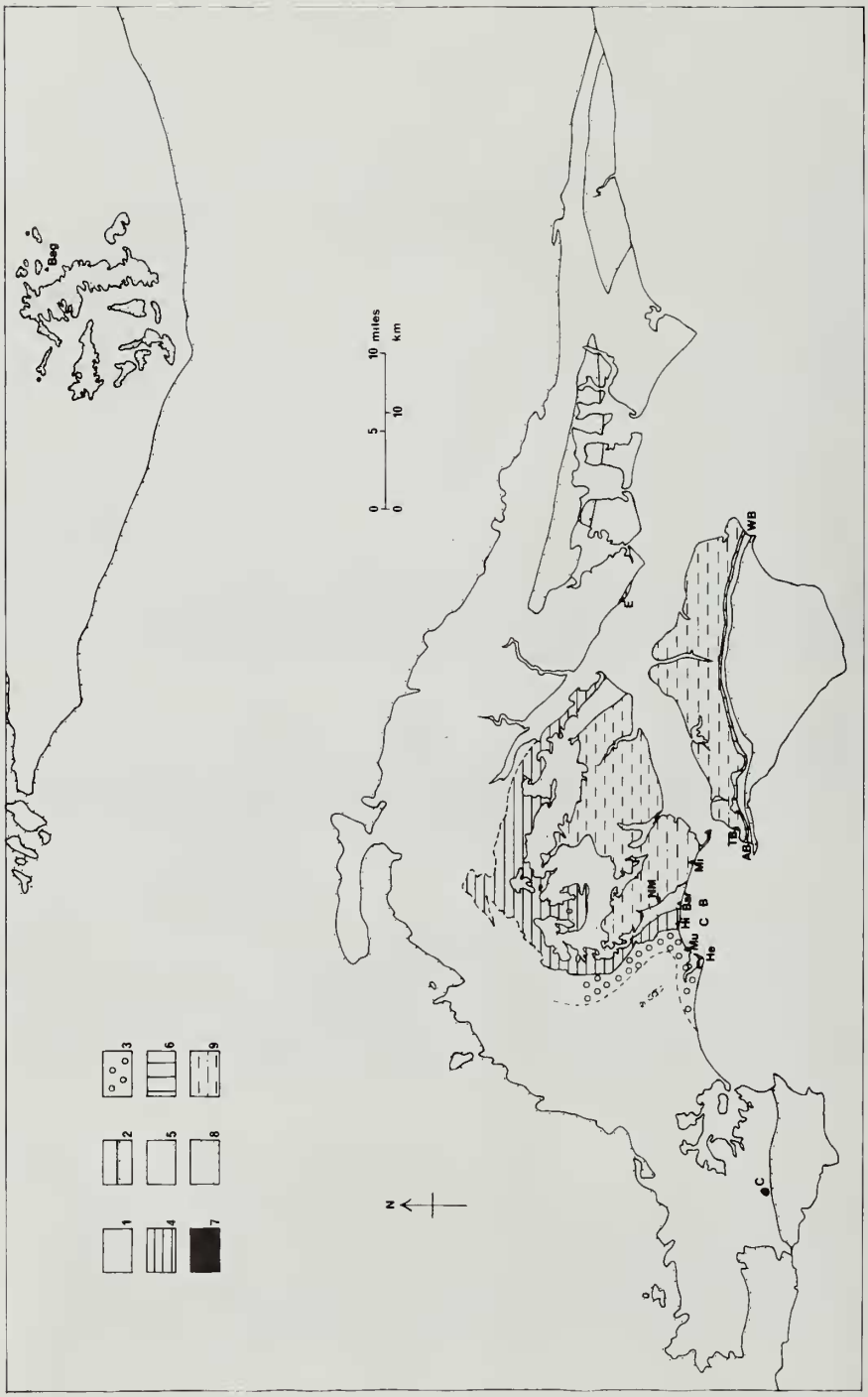
Abbreviations

Institutions and Collections. The following abbreviations are used throughout, appended to mammal specimen numbers, except that Department of Palaeontology, BM(NH), specimen numbers are not given the BM(NH) prefix: they may be recognized either by the prefix 'M' or absence of a prefix for mammalian specimens, and the prefixes GG, In, P, R and V for other biota.

BGS	British Geological Survey, Keyworth and London (formerly Institute of Geological Sciences, London).
BM(NH)	British Museum (Natural History), London.
CGH	Crochard, Girardot, Herman Collection, Brussels, Belgium.
FSL	Faculté des Sciences, Université Claude Bernard, Villeurbanne, Lyon, France.
GH	Geiseltalmuseum, Martin-Luther-Universität, Halle-Wittenberg, D.D.R.
GIU	Instituut voor Aardwetenschappen (formerly Geologisch Instituut), Rijksuniversiteit Utrecht, Netherlands.
GM	Gosport Museum, Hampshire.
IRSNB	Institut Royal des Sciences Naturelles, Brussels, Belgium.
LGM	Musée Géologique de Lausanne, Switzerland (LM = Lausanne Museum, Stehlin's numbering).
MNHN	Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France.
NMB	Naturhistorisches Museum, Basel, Switzerland.
SMC	Sedgwick Museum, Cambridge.
UM	Laboratoire de Paléontologie des Vertébrés, Université de Montpellier, France.
UMMP	University of Michigan Museum of Paleontology, Ann Arbor, U.S.A.

Teeth

I = incisor
DI = deciduous incisor
C = canine
P = premolar
M = molar
DC = deciduous canine
DP = deciduous premolar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Other

L = left R = right
ICZN = International Commission for Zoological Nomenclature.
ISSC = International Subcommission on Stratigraphic Classification.

Localities and stratigraphy

The Bartonian Stage in the concept of continental European palaeomammalogists has comprised the Auversian and Marinesian Substages and it is this period of time which is covered here. The recent restriction of the Bartonian by Curry (1981) is discussed below under correlation, p. 415. Four mammaliferous localities attributed to the Bartonian (one Auversian, three Marinesian, see correlation section) are now known in the Hampshire Basin of southern England. Text-fig. 1 shows the outcrop of Bartonian strata in the London and Hampshire Basins, i.e. upper part of Boscombe Sands; Barton Clay Formation (formally defined here for the first time); Becton Sand Formation (formally defined here for the first time); 'Upper Bagshot Beds'; and Creechbarrow Limestone Formation. Hooker & Ward (1980: tab. 1) show the whole London and Hampshire Basins sequence of vertebrate-bearing Palaeogene strata.

Elmore, Hampshire

This locality is a foreshore exposure just SE of Lee-on-the-Solent, Hampshire (National Grid Reference SU 563001 to SZ 565996). Between here and Stubbington, 3 km to the NW (SU 545018) there is a series of intermittent tidally-controlled exposures of Bracklesham Beds (Selsey and Huntingbridge divisions of Curry *et al.*, 1977). They dip at *c.*2° SW and contain a fully marine invertebrate and fish fauna (see Kemp *et al.* 1979). The strata of the Huntingbridge division at Elmore have been described in detail by Kemp *et al.*, (1979) and named the Elmore Formation. Its lithology is described as 'predominantly interbedded silty clays, clayey silts and sandy silts, usually extensively bioturbated, passing in some areas to a monotonous sequence of clayey silts .... Disseminated fine glauconite is usually present, but medium and coarse glauconite only occurs in the basal 5 m; occasional pebbles have been seen at the basal contact'. It is thus easily distinguished from the underlying 'shelly and nummulitic sandy clays and silty sands of the Selsey division' from which it is separated by a disconformity. Its top is defined by the overlying *Nummulites prestwichianus* bed, which is a biostratigraphic unit, but which is sometimes also lithologically distinctive. Apart from this marker horizon, the Elmore Formation was not clearly distinguished from the overlying Barton Clay by Kemp *et al.* (1979). It is here included as a member within the Barton Clay Formation. (See discussion below under Barton Cliff locality.)

Text-figure 1 Outcrop map of English Bartonian strata. 1 = pre-Bartonian strata. 2 = the edge of the Tertiary outcrops, with the dots outside. 3 = Boscombe Sands. 4 = Barton Clay Formation. 5 = Becton Sand Formation. 6 = Boscombe Sands, Barton Clay Formation and Becton Sand Formation undifferentiated. 7 = Creechbarrow Limestone Formation and unnamed sands below. 8 = Upper Bagshot Beds. 9 = younger Tertiary overlying Bartonian strata. The Upper Bagshot Beds outcrop in the London Basin, the remaining Bartonian and post-Bartonian strata in the Hampshire Basin. The northern edge of the mainland outcrop of the Barton Clay Formation is shown broken. Inclusion herein of the Elmore Formation (Huntingbridge division of the Bracklesham Group) within the Barton Clay Formation means that the basal boundary in this area has not yet been mapped. It is thus shown tentatively, based on information from Studley Wood, Huntingbridge, Marchwood, Dibden, Fawley and Elmore. Small solid triangles indicate towns.

Abbreviations: AB = Alum Bay; Bag = Bagshot; Bar = Barton; C = Creechbarrow; CB = Christchurch Bay; E = Elmore; He = Hengistbury; Hi = Highcliffe; Mi = Milford; Mu = Mudeford; NM = New Milton; TB = Totland Bay; WB = Whitecliff Bay. Sources of data: Reid (1898, 1902*a*, *b*) and White (1915, 1921*a*) and related one inch geological maps; Arkell (1947), Clarke (1981), Gardner *et al.* (1888) and Hooker (1975).

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There are only four mammalian specimens in total. They were surface-collected by Messrs D. J. Kemp and W. J. Quayle and their provenance in the lower part of the Elmore Member (all that is exposed at Elmore) is based on preservation and proximity to the outcrop, coupled with the knowledge that beach material moves little. In support of this last point, the abundant beach-collected Elmore shark fauna retains its individuality from that of Long Bank, Lee (Selsey division), less than 1 km to the NW (see Kemp *et al.* 1979: 95).

Hengistbury, Dorset

This locality is a sea cliff about 1·5 km long and a maximum of 35 m high, on a promontory known as Hengistbury Head (SZ 1790). It comprises, from below upwards: Boscombe Sands, Barton Clay Formation (formerly known as Hengistbury Beds) and unnamed sands (incorrectly called Highcliff Sands by Gardner (1879) but herein tentatively referred to the Becton Sand Formation (q.v., p. 205). Historical reviews as well as detailed sections and faunal lists were given by Hooker (1975) and Curry (1977). The only mammalian specimen from this locality is, according to preservation, from the 'Hengistbury Beds' (Hooker 1977*a*). The 'Hengistbury Beds' are sandy clayey silts to clayey silty sands with pebble beds, richly glauconitic in the lower part and with siderite nodules in the upper part, with a shallow marine invertebrate and fish fauna. They are here formally included in the Barton Clay Formation (see below under Barton Cliff locality) following Prestwich's (1849) identification, but within which they probably require separate member status. Final evidence that the 'Hengistbury Beds' are lateral equivalents of and do not dip below the Barton Clay has been provided by the Christchurch borehole (Freshney & Edwards 1983). It shows Barton Clay and the subjacent Boscombe Sands to rest directly on a thick sequence of non-glauconitic sands with interbedded clays and lignites.

Barton Cliff, Hampshire

Introduction. The sea cliffs of Christchurch Bay from Christchurch Harbour in the west to Milford-on-Sea in the east are up to 30 m high and divided into four stretches by river valleys, the steep-sided ones being locally known as bunnies. The second stretch from the west is delimited westwards by Chewton Bunny (marking also the Hampshire–Dorset border) and eastwards by Becton Bunny and is known as Barton Cliff. Barton-on-Sea is situated about midway along its length. The strata in Christchurch Bay dip fairly regularly and very gently (*c.*2°) NE. In upward stratigraphic succession are exposed: the Boscome Sands, Barton Clay Formation, Becton Sand Formation (both defined here), Lower Headon Beds and basal unit of the Middle Headon Beds. The brackish to freshwater Lower Headon Beds in this section contain a well-known early Ludian mammal fauna at Beacon and Hordle Cliffs. At least three levels in the Barton Clay, at 35 m, 40 m and 48 m below the base of the Headon Beds, contain a few important marine and terrestrial mammals (Pl. 1; Text-fig. 2; Halstead & Middleton 1972; Hooker 1972).

Lithostratigraphy of the 'Barton Beds' – Historical background (see Text-fig. 3). As recorded by Curry (1958*a*), the term 'Barton Clays' was coined by Prestwich (1847: 355) for the 'clays of Barton'. Prestwich (1846) and previous authors (see Prestwich 1846: 224–226) had considered these clays to be part of the London Clay. Although the type locality of the Barton Clay is

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Plate 1 Sections in Barton Clay Formation, Barton Cliff, Hampshire. For scale, see bed thicknesses in Text-fig. 2, p. 201.

Fig. 1 Wave-washed lowest cliff terrace between Chewton Bunny and Barton-on-Sea. Beds A3 to D are shown. Bed C is delimited by nodule bands (n) and is also marked by a central, prominent, light-coloured non-glauconitic clay band. Talus (t) moves on a slide plane (s) over the lowest part of bed D.

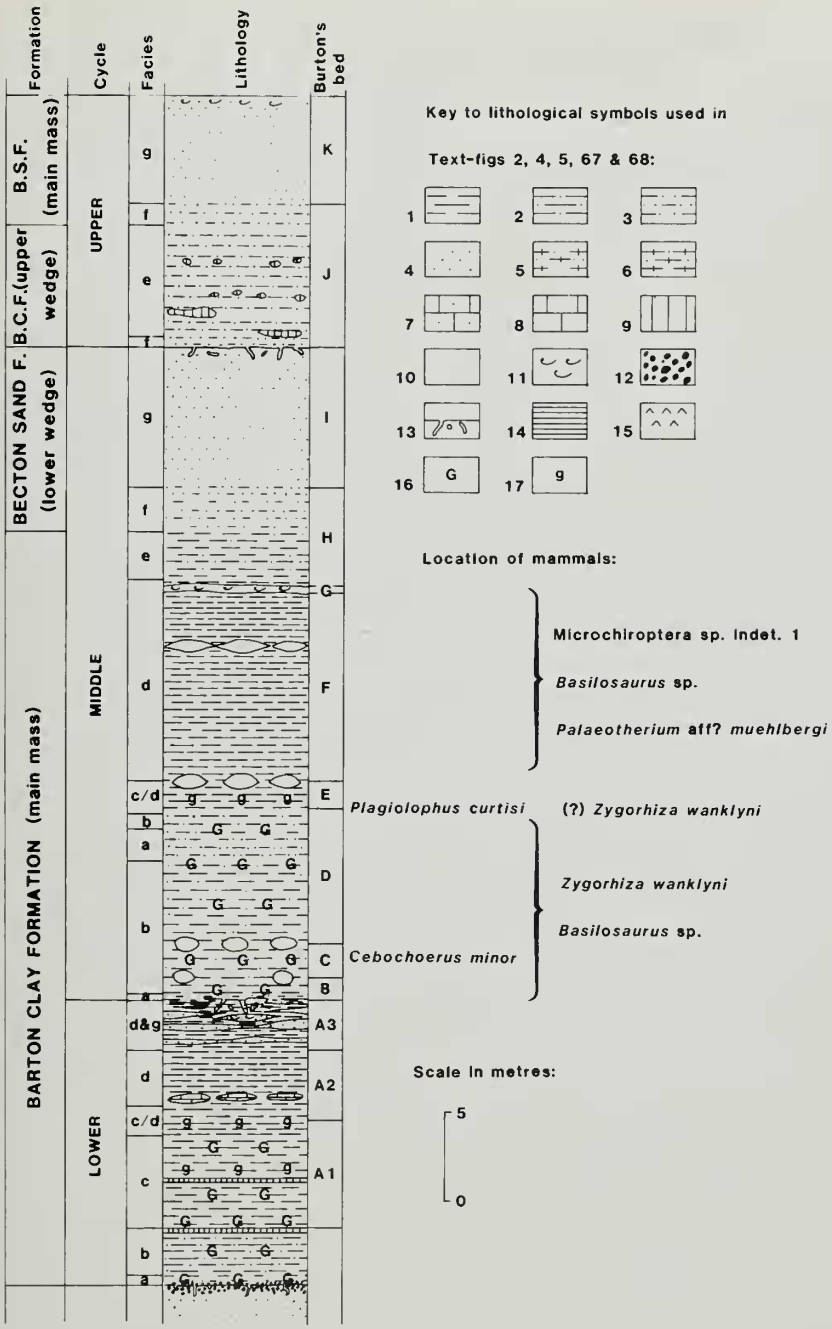
Fig. 2 Upper cliff terraces between Chewton Bunny and Barton-on-Sea. Beds E to F are shown, capped by Pleistocene plateau gravel (g). Nodule bands (n) separate beds E and F and also upper and lower parts of bed F.

Barton Cliff, most of Prestwich's attention to this stratigraphic unit was focused on Alum and Whitecliff Bays on the Isle of Wight, as these are the localities at which he had drawn up his detailed sections in 1846. At Alum Bay, Prestwich's Barton Clay is easy to define because it is sandwiched between two sand units and there is a prominent pebble bed at the base. The upper sands, termed Headon Hill Sand by Prestwich (1846: 243) are succeeded everywhere by what has long been known as the Fluvio-marine series (Prestwich 1846: 243). In Christchurch Bay, however, a bed of clay divides the upper sands into two parts. As Curry (1958*a*: 14) noted, it is not clear whether the top of the Barton Clay at the type locality is at the top of this clay bed or lower down at the top of the main mass of clay. Moreover, it does not appear that at the time Prestwich was very well aquainted with the Barton section as he did not specify this particular point. In a later work, however (Prestwich 1857: 108), it is evident that the junction was intended to be the lower of the two alternatives.

Prestwich (1857: 108) used the term 'Barton series', comprising the Barton Clay and Headon Hill Sand. Fisher (1862: 86–91) raised the base of the Barton Series in Alum Bay from the pebble bed of the original definition to the *Nummulites prestwichianus* bed, about 14 m above, relegating the strata below to the Bracklesham Beds. Keeping (1887: 71) recognized the *N. prestwichianus* bed in Whitecliff Bay. Gardner *et al.* (1888) divided the Barton Beds (=Series) into Lower, Middle and Upper on the basis of faunal changes through the sequence. The Geological Survey in mapping used the terms Barton Clay and Barton Sand, the latter to replace Headon Hill Sand (Reid 1898: 30). Burton (1929) further divided the Barton Beds into thirteen lettered beds with an additional fourteenth (L) which referred to the Lignite Bed which Gardner *et al.* (1888: 596, fig. 4) considered to commence the Headon Beds. Burton based his beds or 'horizons' on faunal content but they often coincided with distinct lithologies and their limits were defined using lithological markers such as nodule bands (e.g. see Pl. 1). Curry (1958*b*: 12) returned to Prestwich's concept of the base of the Barton Beds in Christchurch Bay, as this was 'the natural break in the succession'. No major changes were then made until Stinton (1975), in order to comply with the Stratigraphical Code of the Geological Society of London (Harland *et al.* 1972, which differs little from Hedberg, 1972, 1976) created the term Barton Formation, incorporating the Barton Beds of Prestwich plus the Lower Headon Beds.

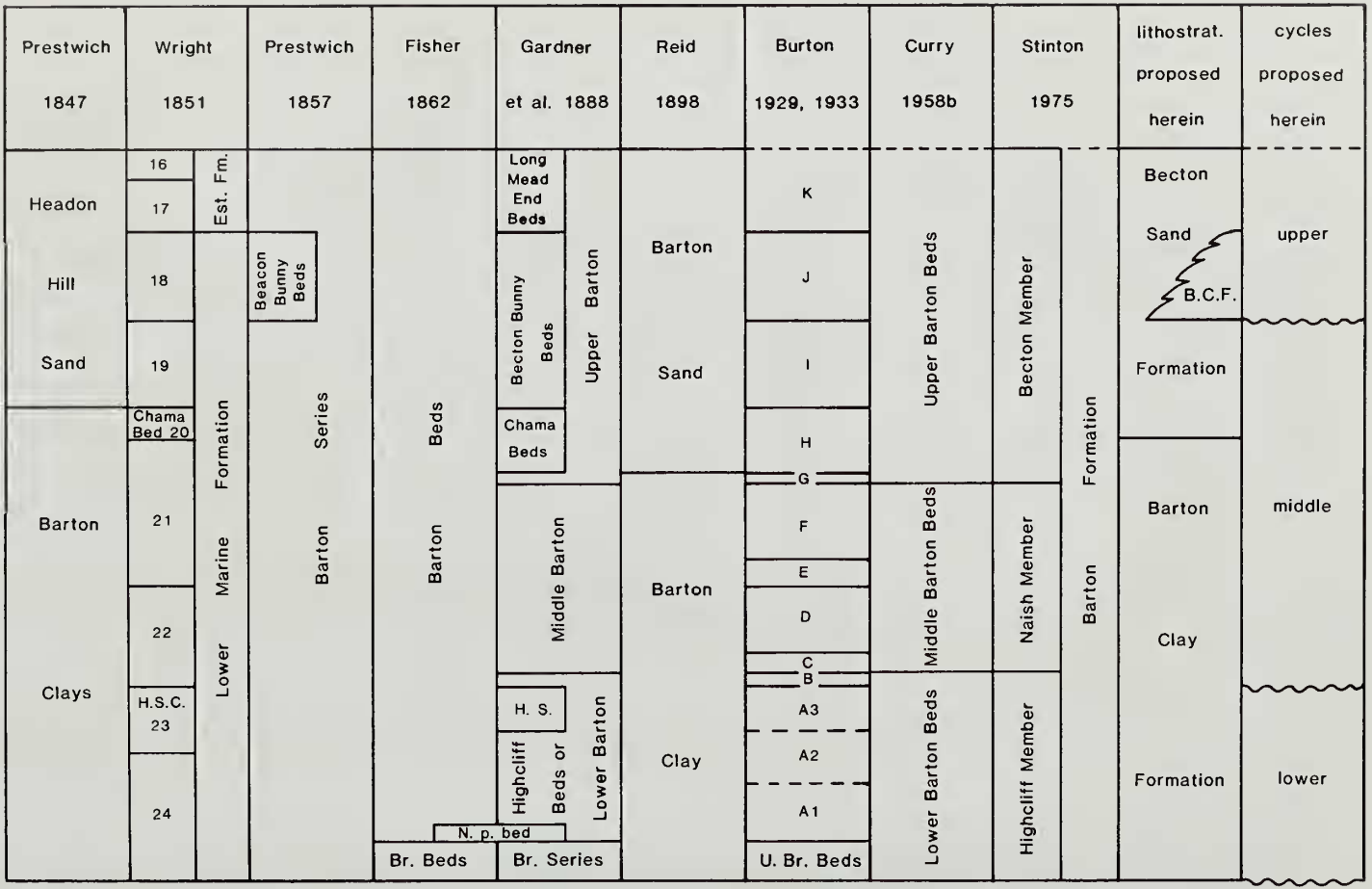
Lithostratigraphy of the 'Barton Beds' – Interpretation. Prestwich's (1847) first attempt to define the Barton Clay and Headon Hill Sand involved lithostratigraphic considerations. He ignored fauna except to show that the Barton Clay was not the same age as the London Clay. The subsequent altering of the lower limit of the Barton Clay (Fisher 1862, Keeping 1887) was based essentially on a fossil occurrence: that of *N. prestwichianus*, although Fisher also referred to lithological differences. Likewise the threefold division of Gardner *et al.* (1888) was based on biostratigraphy. Burton's system, whilst being claimed as faunal in the title of his 1933 paper, was really a composite of biostratigraphy and lithostratigraphy. Stinton's (1975) Barton Formation was stated to follow Curry (1958*a*). However, Curry (1958*a*: 14) in the section dealing with Barton Beds upheld the limits and divisions of Gardner *et al.* and Burton. Nevertheless, he used (Curry 1958*a*: 5) the term 'Bartonian Stage' (chronostratigraphy) to comprise the time of deposition of both the Barton Beds and the Lower Headon Beds (different lithostratigraphic entities), and this may be what Stinton meant. In fact, as Stinton described it, the Barton Formation coincides exactly with the Bartonian cycle of Stamp (1921: 153). Sedimentary cycles or cyclothems are stated by Hedberg (1972: 305; 1976: 36) to be informal terms for the purposes of international stratigraphy and therefore not to form the basis of lithostratigraphic terminology. The Barton Formation has therefore no lithostratigraphic foundations, nor moreover have its included members, which coincide with the biostratigraphically-based Lower, Middle and Upper divisions of the Barton Beds of Gardner *et al.*, plus the lower division of the Headon Beds. See also comments by Daley *et al.* (1979) and Stinton & Curry (1979).

The original limits of the Barton Clay and Headon Hill Sand (Prestwich 1846, 1847) correspond closely to a basic lithostratigraphic breakdown of the sequence concerned. This fact is emphasized by Curry's (1958*a*: 14) statement: 'In areas where the Barton Beds are unfossiliferous, a lithological division into Barton Clays below (corresponding roughly to the



Text-figure 2 Stratigraphical column of Barton Clay and Becton Sand Formations in Christchurch Bay. Occurrences of mammals are indicated; those on left are located with precision; those on right are located approximately according to preservation and locality data.

Key to symbols: 1, silty clay; 2, sandy silty clay; 3, clayey silty sand; 4, sand; 5, calcareous sand; 6, sandy marl; 7, sandy limestone; 8, limestone; 9, siderite; 10, 'claystone' (?phosphatic); 11, shells abundant; 12, pebbles/cobbles; 13, burrowed horizon; 14, lignitic, often laminated clay; 15, gypsum; 16, major glauconite occurrence; 17, minor glauconite occurrence.



Text-figure 3 Contrasting classifications of strata in Christchurch Bay here referred to the Barton Clay and Becton Sand Formations. Abbreviations: B.C.F. = Barton Clay Formation (upper wedge); Br. = Bracklesham; Est. Fm. = Estuary Formation; H.S. = Highcliff Sands; H.S.C. = High Cliff Sands and Clays; N.p. = *Nummulites prestwichianus*.

Lower and Middle Bartons) and Barton Sand(s) (Upper Bartons) above has been used'. White (1921*a*: 98) considered the term Headon Hill Sands to have been superseded by Barton Sand; in fact its abandonment avoids potential confusion with the Headon Beds.

In order to conform with the correct application of the procedure for international stratigraphy, it is here proposed that Barton Clay Formation and Becton Sand Formation be used for Prestwich's Barton Clays and Headon Hill Sand respectively, and that the use of the term 'Barton Formation' with its included members (Stinton 1975) be discontinued. This proposition both follows the new system and maintains as far as possible original definitions, providing mappable units which are a prime requisite of geological formations.

Formal Designation of the Barton Clay Formation

i. TERM: Barton Clay Formation.

ii. STATUS: Formal lithostratigraphic unit.

iii. STRATOTYPE LOCALITY: Cliff sections in Christchurch Bay from Friar's Cliff, Mudeford in the west to just east of Barton-on-Sea in the east.

iv. GRID REFERENCE: SZ 194927 to SZ 242927.

v. HYPOSTRATOTYPES: Cliff sections in Alum Bay (SZ 305854 to SZ 304855) and Whitecliff Bay (SZ 641862 to SZ 642863). Both show sequences more chronologically extended in Barton Clay lithology than does the stratotype.

vi. LITHOLOGY. Grey to brown silty, usually shelly (but sometimes decalcified), sometimes medium to very fine sandy, clay, with subordinate clayey sandy silts. Glauconite occurrence varies from abundant large unrolled grains to absent. The glauconitic beds contain irregular patches of very coarse subangular sand. Subsidiary beds of very fine sand also occur. There are several layers of calcareous, phosphatic and sideritic nodules. The sediments are strongly bioturbated except for the sand lithology, which is laminated and shows lenticular bedding. At the western (Hengistbury) end of the depositional basin, the sediments contain more sand and silt and less clay than at the type and most other localities. The clay mineralogy is dominantly an illite/kaolinite suite, although mainly illitic/smectitic in the Elmore facies (see Curry *et al.* 1968; Gilkes 1968, 1978; Blondeau & Pomerol 1969). Two sharp junctions occur within the formation between cyclothems (described below). Rolled flint pebbles occasionally occur through the main mass, becoming common in the extreme west, and rolled flint cobbles and/or pebbles tend to form a basal bed.

vii. BIOTA. An abundant marine invertebrate fauna, especially molluscs, and a notable shark tooth and teleost otolith fauna. Marine and land-derived tetrapods, as well as the fruits, seeds, cones and wood of land plants also occur. The most up-to-date comprehensive list is by Burton (1933). Subsequently, numerous specialist papers have appeared which include studies of organisms from the Barton Clay; these include foraminifera (Curry 1937, Murray & Wright 1974), brachiopods (Elliott 1954), molluscs (numerous papers by Wrigley; see list in Cox 1954), ostracods (Keen 1978: 439), malacostracan crustaceans (Quayle & Collins 1981, Quayle 1982), asteroids and ophiuroids (Rasmussen 1972), fish otoliths (Stinton 1975–80), sharks (Ward 1980), turtles (Moody 1980), birds (Walker 1980), marine mammals (Halstead & Middleton 1972), calcareous nannoplankton (Martini 1971, Aubry 1983), dinocysts and acritarchs (Bujak *et al.* 1980), palynomorphs (Gruas-Cavagnetto 1970), and macroplants (Chandler 1960, 1978). Some of the bivalve molluscs (e.g. *Psammotaea*) can be found in vertical life position in the sediment, whereas many other molluscs show evidence of having been buried as long dead shells colonized inside or out, or both, by bryozoans, oysters, serpulid worms and the gastropod *Capulus*, etc.

viii. THICKNESS. Approximately 40 m at Barton Cliff. It is *c.* 74 m at Alum Bay and *c.* 60 m at Whitecliff Bay. The latter is calculated at 90° to the strike; note that Gardner *et al.*'s (1888: 604) measurement of 368 ft 1 in (*c.* 112 m) for the sequence of the *N. prestwichianus* bed to the top of the Barton Sand must have been taken directly from the cliff section which is oblique to the strike. They noted that 'the section is not quite at right angles to the outcrop, and a diagonal direction may somewhat exaggerate the thickness' but apparently made insufficient allowance

for this. The true measurement for this sequence is 97 m (*c.* 318 ft). The thickness at Alum Bay is probably exaggerated by tectonic disturbance (see Curry 1942: 99).

ix. RELATIONSHIPS. a. *Position of the basal junction.* The base bed of very glauconitic clayey sand to silt rests sharply, usually with a basal pebble bed, on different horizons of the light-coloured Boscombe Sands or non-marine lignitic clays in the west, and on more kaolinitic shelly sandy clays and clayey sands of the Selsey division (Bracklesham Group) (see Curry *et al.* 1968: fig. 4) in central and eastern parts of the area of deposition.

b. *Evidence.* Kemp *et al.* (1979) erected the Elmore Formation for the strata between the shelly sandy clays of the Bracklesham Beds (Selsey division) and the *N. prestwichianus* bed of the Barton Clay in Whitecliff Bay, but excluded the clays between the pebble bed and the *N. prestwichianus* bed in Alum Bay as being a different facies.

Two main problems are posed here by the Elmore as a formation. Firstly, it was described from a detailed section at Elmore, but as only the lower part was exposed at this locality, Whitecliff Bay was chosen as the type locality. Unfortunately no detailed section has ever been published of this part of the sequence in Whitecliff Bay, as it is normally vegetated in the cliff and obscured by beach material on the foreshore (see Prestwich 1846, Fisher 1862, Gardner *et al.* 1888). Recently the author had the opportunity of examining a freshly scoured exposure at the cliff foot, which showed an almost complete sequence of green, poorly glauconitic clays and silts, for about 10 m below blue clays with *Nummulites rectus*. The occurrence of *N. prestwichianus* in a richly glauconitic sand layer in the cliff, however, could not be traced to the cliff foot and may be cut out by a fault, parallel with the strike, which is visible at about the appropriate horizon (*c.* 6 m below *N. rectus* according to Curry *et al.* 1972). Nevertheless there appeared to be no change in lithology upwards from typical Elmore facies until the *N. rectus* clays were reached. Secondly, the Elmore Formation includes beds of richly glauconitic sand and sandy clay with coarse quartz grit at its base (e.g. Studley Wood and Huntingbridge). These are very similar to beds at Alum Bay and Hengistbury which were expressly excluded from the formation by Kemp *et al.* (1979), but included in Prestwich's definition of Barton Clay.

Thus the Elmore facies appears no more distinct than any of the other various minor facies which occur within the Barton Clay; and it is more appropriate to include it within the Barton Clay Formation as a member than treat it as a formation in its own right. This procedure, moreover, does not contravene historical precedent. Fisher (1862: 80) noted that 'the character of the matrix at Hunting Bridge approaches more nearly to some of the Barton deposits than to any of the Bracklesham strata'. It was only the fossils that caused him to state 'the species are so decidedly of a Bracklesham type, that I have no hesitation in classing the deposit as a part of that series'. It is easy to separate Fisher's biostratigraphy from his lithostratigraphy. Prestwich (1847) too included the upper part of the Huntingbridge division in Alum Bay in his original concept of the Barton Clay (see Fisher 1862: 87–91, and Text-figs 67–68 herein, for correlation). It seems therefore that the basal junction of the Barton Clay is successively younger when one traces it from Whitecliff Bay to Alum Bay and from there to High Cliff and Hengistbury (see Text-fig. 68 for its base at the different localities).

c. *Position of the top junction.* Where bed J is absent, the top is the transitional boundary from predominantly clay to predominantly sand within the middle cyclothem (see below); i.e. the middle of Burton's bed H, below the Chama Bed (*sensu stricto*). Where bed J is present, the top is within the upper cyclothem, the transitional boundary from predominantly clay to predominantly sand near the top of bed J. To the west (Hengistbury) the Barton Clay Formation (lower part) seems to be beginning to pass laterally into a sandy, pebbly unit, but is then truncated by modern erosion (Hooker 1975).

d. *Evidence.* In Whitecliff Bay, the upper part of the Barton Clay was called 'Chama Bed' by Gardner *et al.* (1888), in allusion to one of its shelly fossils and equivalent position in the lithological sequence to that at Barton. They noted, however, that it appeared more clayey than at the type locality. In fact, it consists of dark grey clays, becoming sandy upwards and with small tabular or irregularly ovoid siderite nodules. Its lithology thus resembles Barton bed J. It

rests with a sharp junction on blue-grey sandy clays, which are correlated on dinocyst evidence (Bujak *et al.* 1980) with the sequence upper bed H–lower bed I at Barton. The best time correlations here are of the Whitecliff Bay 'Chama Bed' with Barton bed J and of the immediately underlying sandy clays in Whitecliff Bay with Barton bed I. This suggests that the sand lithology of bed I has wedged out eastwards or northeastwards. It is thus logical to include bed J at Barton in the Barton Clay Formation, despite Prestwich's (1857) decision, in view of the above evidence.

x. DISTRIBUTION: Limited by the area of outcrop in the Hampshire Basin. Main sections recorded: Barton Cliff, Alum Bay, Whitecliff Bay (Gardner *et al.* 1888), Hengistbury (Curry 1977; Hooker 1975); Studley Wood (Stinton 1970); Huntingbridge and Elmore (Kemp *et al.* 1979). Former sections: Afton, Gunville (Curry 1942), Hinton Admiral (Gardner *et al.* 1888), Bransgore, Poulner, Totton (Burton 1933), Fawley (Curry *et al.* 1968), Marchwood. Also numerous wells and boreholes (Whitaker 1910, 1917; Freshney 1978).

xi. AGE: Bartonian (Auversian plus Marinesian) to earliest Ludian?, late middle/late Eocene.

xii. SYNONYMY: Approximately equal to the Barton Clay of Prestwich (1847). Comprises Burton's (1929, 1933) beds A1 to H (lower half) and J (= Beacon Bunny Beds of Prestwich, 1857) plus the beds between the base of A1 and the pebble bed, all in Christchurch Bay. Includes Hengistbury (Head) Beds of Gardner (1879) as western unit and Elmore Formation and Huntingbridge bed(s)/division as eastern unit within the lower part of the formation. Equals the lower part of the Barton Beds/series of authors. Includes the Highcliff Sand and Clay of Wright (1851) (= A3; not the Highcliff Sand of Gardner, 1879).

Formal Designation of the Becton Sand Formation

i. TERM: Becton Sand Formation. Derived from Becton Bunny which divides Barton Cliff from Beacon Cliff and on either side of which occur the strata defined. The name is also chosen as the Formation nearly coincides with Stinton's (1975: 7) informal Becton member. Although the term Barton Sand is well known (see views of Lawson 1979), the concept of a formation distinct from the Barton Clay is considered to be best achieved by avoiding name repetition. The concept of the Barton Beds as a whole is non-lithostratigraphic and requires other definitions.

ii. STATUS: Formal lithostratigraphic unit.

iii. STRATOTYPE LOCALITY: Cliff sections in Christchurch Bay from west of Sea Road Gap in Barton Cliff to the west, eastwards to Long Mead End (Taddiford Gap) at the eastern extremity of Beacon Cliff.

iv. GRID REFERENCE: SZ 229931 to SZ 262922.

v. LITHOLOGY. Fine sands, largely decalcified, clayey and silty at the base. Glauconite is absent or sparse and fine-grained. Mica is frequent especially towards the top. The sediments are strongly bioturbated and, especially in the lower sand unit, display abundant pellet-lined burrows of *Ophiomorpha*. Rolled flint pebbles occur at the base of a clay unit in the upper part in the east of the basin (Whitecliff Bay). One sharp junction is sometimes recognizable within the formation in the west, between the middle and upper cyclothems, as a slightly indurated ferruginous band (Alum Bay). Division into two wedges occurs through interdigitation with bed J of the Barton Clay Formation. At Barton Cliff the latter is seen to pass laterally westwards into sand of the same facies as bed K. The transition takes place over a distance of about 1 km and the interlocking tongues of sand and clay are complicated by prominent dewatering structures.

vi. BIOTA. This is generally sparse but essentially rather similar to that of the Barton Clay Formation and many of the references given there will suffice here. The biota is, however, more restricted, especially in the upper part which is less marine. No mammals are known.

vii. THICKNESS. 25 m at Barton Cliff; 27·4 m at Alum Bay (according to Curry & Edwards, 1972, but subject to the same tectonic disturbance as the Barton Clay Formation at this locality); and 55 m in Whitecliff Bay (see comment on previously published thickness under definition of Barton Clay Formation, pp. 203–204).

viii. Relationships. Rests with transitional, partially interdigitating, contact on Barton Clay Formation. The top is overlain sharply by the Lower Headon Beds. At the type locality the overlying bed is a thin green sandy clay, uppermost bed K of Burton (1933). This is overlain by a thick shelly lignitic clay (described as bed L of the Barton Beds by Burton (1929) and as the lignite bed of the Lower Headon Beds ('Lower Freshwater Formation') by Wright (1851)). The lignitic clay bed was treated as two different beds by Stinton (1975: 7). Rootlets descend from this horizon into the beds below.

ix. Distribution: Limited by the outcrop in the Hampshire Basin. Main sections: Barton and Beacon Cliffs (Burton 1929, 1933), Alum Bay, Whitecliff Bay (Gardner *et al.* 1888), Warwick Slade (Stinton 1970), Totland (Fowler *et al.* 1973). Former sections: Poulner, Fawley (Burton 1933), Brockenhurst (White 1921*b*). Also numerous wells and boreholes (Whitaker 1910, 1917; Freshney 1978).

x. Age: Late Bartonian (? Marinesian) to early Ludian?; late middle/late Eocene.

xi. Synonymy: Equivalent almost exactly to Headon Hill Sand (Prestwich 1846), Barton Sand (Reid 1898) and Upper Bagshot Sand of Tawney (1882). Includes Barton Beds/series in part and comprises Burton's (1929, 1933) beds H (upper) (= Chama Bed s.s.), I and K, except uppermost green clay. Also includes the lower part of the Becton Bunny Beds (Gardner *et al.* 1888) and the Long Mead End Sands (Tawney 1882).

Sands above the 'Hengistbury Beds'. These at Hengistbury may tentatively be included in the Becton Sand Formation as a third, lowest wedge (see Text-fig. 68), but it cannot be confirmed that it was once continuous with known parts of the formation.

Discussion of B.G.S. concept. The current concept of the Barton Formation, as developed by the B.G.S. in the course of mapping the Southampton sheet, is as follows. It comprises Barton Sand, Barton Clay, Huntingbridge division (including Elmore Formation) and sandy clays with *Nummulites variolarius* near the top of the Selsey division (Bracklesham Group). They divide the Barton Formation into a Becton Sand Member (= Barton Sand) and a Barton Clay Member (= the rest) (E. Freshney, personal communication 1981).

Their Barton Formation is, however, mainly a cyclothem and so does not constitute a formation in Hedberg's (1976) sense. Moreover, inclusion of the Selsey division clays causes problems. Sandy clays are interspersed with sandy silts and silty sands in the Selsey division at several levels and localities, not just at the top. Those at the top resemble those lower down in being shelly and having the same clay mineralogy (Curry *et al.* 1968). On the basis of detailed lithology, the latter would have to be included also, and distinctions from the Bracklesham Group would break down. The characteristics of the Barton Clay Formation as a glauconitic or non-glauconitic silty clay with only subsidiary glauconitic clayey sands are important, as are those of the Bracklesham Group as glauconitic sands and sandy clays with intercalated laminated non-glauconitic clays. Curry *et al.* (1968) distinguished three facies in the Fawley Transmission Tunnel and the marked change from the second to the third facies was between the Selsey and Huntingbridge divisions (see Kemp *et al.* 1979). This would thus seem the most appropriate position to place the Bracklesham Group–Barton Clay Formation boundary.

Cyclothems in Christchurch Bay (Text-fig. 2). Two sharp breaks with erosive bases occur in the sequence of the Barton Clay and Becton Sand Formations. They separate three somewhat similar sequences of sediments. The sharp breaks occur at the junctions of Burton's beds A3/B and I/J. The complete idealized sequence of facies is as follows: glauconitic clayey sand/silt (a); glauconitic sandy silty clay (b); glauconitic silty clay (c); non-glauconitic silty clay (d); non-glauconitic sandy silty clay (e); non-glauconitic clayey silty sand (f); and non-glauconitic sand (g). The middle sequence is complete, the lower sequence is almost complete whilst the upper only consists of the last three facies. All three coarsen upwards and therefore in part form similar cyclothems (cycles). The gradual changes within each cycle make the boundaries between Burton's beds (except those coinciding with cycle boundaries) difficult to define, especially when nodule bands or oyster beds are impersistent (e.g. in a restricted section). Certain

detailed differences are noticeable between the three cycles. In the lower, the change from one lithology to the next occurs initially by intercalation of a thin bed of the new type. This is followed by further intercalations which become steadily thicker until they exceed and finally exclude those of the old type. In fact in the lower cycle the non-glauconitic sand facies occurs only as intercalations with non-glauconitic silty clay (the non-glauconitic sandy clay facies being cut out); the former never excludes the latter. The middle cycle undergoes only gradual lithological changes, as does the upper. The middle cycle also has a sequence of four nodule bands. The nodules in the first and second bands (B/C and C/D junctions) are subspherical to subovoid; those of the third (E/F junction are subovoid/lenticular; and those of the fourth (within F) are lenticular. Moreover, the Stone Band (G) could be regarded as the final expression of this shape trend, as it is a semi-continuous tabular layer. A slight interruption to the otherwise steady sequence of the middle cycle is the glauconitic sandy interval in the middle of D.

The junction of the Barton Clay and Becton Sand Formations is difficult to recognize. A lithological boundary has previously been taken above the Chama Bed (H) and below the overlying decalcified sands (I). However, when weathered and leached (as at the top of Barton Cliff) the upper part of H appears more sandy and light-coloured and is difficult to distinguish from overlying bed I. To overcome this problem, the formational boundary has been placed at the point where sand first predominates in the sediment. This is roughly in the middle of bed H (base of Chama Bed s.s.) for the lower sand wedge (I) and the top of bed J for the upper sand wedge (K).

The sharp junctions between the lower and middle and between middle and upper cycles have been modified by penecontemporaneous burrowing organisms, so that in places the junctions appear indistinct at close range. These burrows occur throughout the sequence, but are more easily seen at sharp lithological junctions. The burrows often have lined walls (*Ophiomorpha*), which may show glauconite or limonite enrichment. The large burrow systems from the base of B penetrate well into A3, disturbing the sediment, and often contain fossils from B which have thus been introduced secondarily into A3. To further complicate matters, in the lower part of B, some rolled shells occur with patchy black staining which is a preservation diagnostic of A3. It appears that they were derived into B following a phase of erosion which removed the top of A3.

The regressive phase of the upper cycle is continued through the overlying Lower Headon Beds, where the overall facies is non-marine (see Plint (1984) for stratigraphic and sedimentological coverage).

Creechbarrow, Dorset

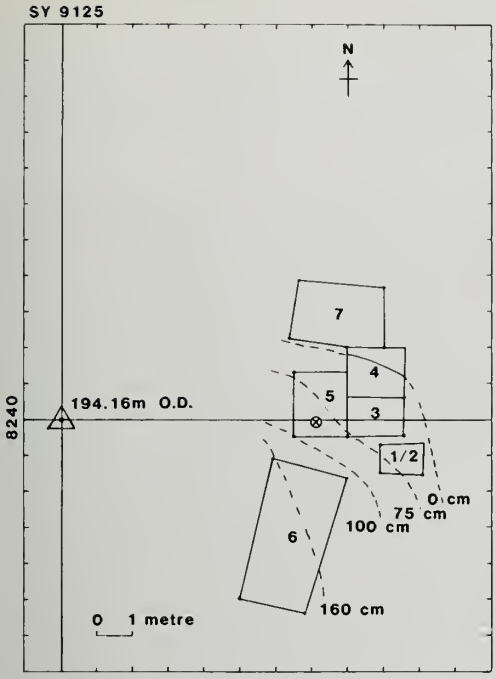
Of the four localities, this one has yielded by far the largest number of mammalian specimens. On Creechbarrow Hill (SY 921824) over 80 m of clays, sands and conglomerates overlie the 'Dorset Pipe Clay series' and are capped by the Creechbarrow Limestone Formation (Hooker 1977*b*). The mammal fauna is from the latter. The deposits above the pipe clays occur as an outlier and are only known to outcrop on Creechbarrow Hill. There are no natural exposures, so knowledge of the succession is limited to mines in the pipe clays, old pits in the pebbly sands (Hudleston 1902*a*, 1903; Arkell 1947), temporary excavations in the Creechbarrow Limestone and a borehole (Pl. 2; Text-figs 4–6).

Arkell (1947: 233–241) reviewed the history of investigations at the site to that date, but it was not until 30 years later that the limestone was shown to be Bartonian rather than Ypresian ('Lower Bagshot') or Ludian (Bembridge Limestone) in age (Hooker 1977*b*). Hooker (1977*b*) and Preece (1980*a*) also summarized the history of the site.

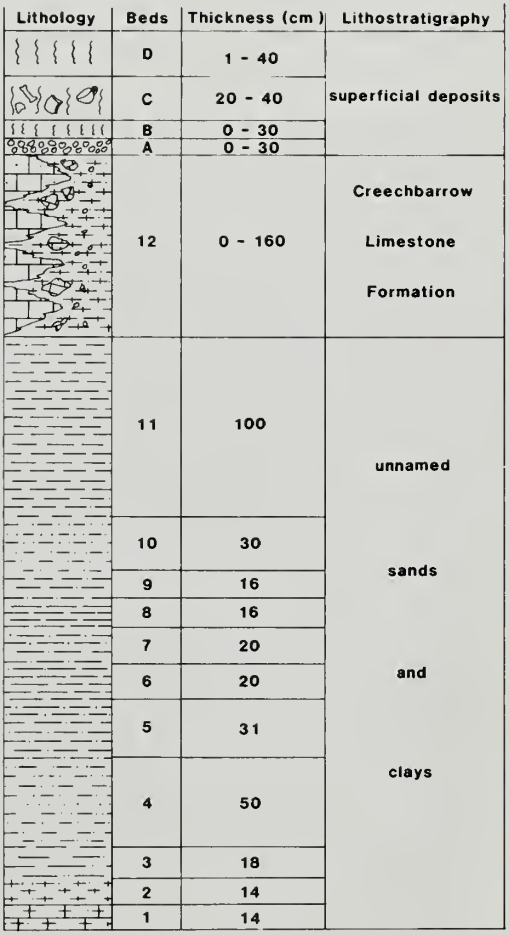
The succession near the summit. Hudleston's (1902*a*, 1903) descriptions of the succession as exposed in small, now overgrown, pits are detailed, although unfortunately he saw no need to publish a map of these (Hudleston 1902*b*: 169, footnote). The lithic descriptions here are limited to the exposures made between 1975 and 1978 in the region of the limestone for the purpose of collecting its biota (see Text-fig. 5).

1

2



Text-figure 4 Map of recent Creechbarrow excavations. Spot height of trigonometrical point at summit of the hill is shown. Excavation holes 1 to 7 are numbered. The position of the hand-cored borehole in hole 5 is indicated. Isopachytes of the Creechbarrow Limestone Formation are given.



Text-figure 5 Stratigraphical column of strata exposed in the recent Creechbarrow excavations. For key to lithological symbols of solid deposits, see Text-fig. 2, p. 201. For description of superficial deposits, see p. 211.

The Creechbarrow Limestone Formation. This comprises bed 12 (see Text-fig. 5), a buff marl containing variable sized limestone clasts.

The limestone (sensu stricto): a cream coloured, mottled with buff, soft to hard, massive micritic limestone with drusy sparite, scattered angular to subangular quartz grains up to *c.* 1 mm diameter, oncoliths often containing gastropods (Hudleston's 'horseshoe concretions'), occasional slug plates, moulds of land snails and vertebrate remains. Hard limestone in the recent excavations was mainly encountered in the basal rubbly soil layer (A). None of the

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Plate 2 Creechbarrow, Dorset.

Fig. 1 General view from the south-west. The outcrop of the unnamed sands, clays and gravels is marked by the dark cover of bracken (*Pteridium aquilinum* (L.)). The outcrop of the Creechbarrow Limestone Formation at the summit is marked by the light cover of grass.

Fig. 2 Section in north-east corner of Hole 6. For explanation of bed numbers see Text-fig. 5 (above) and text. Scale is in centimetre units.

limestone appeared to be truly *in situ*, although Hudleston (1902*a*: fig. 2) claimed to have found it so in his 'summit pit'.

The buff marl: a buff calcareous silty clay with abundant angular to subangular quartz grains up to 1 mm diameter and containing limestone clasts (see above). It also contains oncoliths often containing gastropods, snail opercula, slug plates, vertebrate remains and derived silicified Cretaceous bryozoans.

Interpretation of bed 12. The size and abundance of limestone clasts within the buff marl increases towards the centre of the summit of the hill, until it finally consists of a mass of large limestone boulders with the marl simply filling the narrow gaps in between. This suggests that the marl may be the result of decomposition *in situ* of softer parts of the limestone.

A piece of soft limestone was broken down in dilute acetic acid and yielded a very poorly sorted sand with minor silt and clay components and vertebrate debris. The greater proportion of clay which occurs in the marl suggests that the above interpretation of the origin of the marl is too simple. It is perhaps more likely that there was originally a series of passage beds from manganiferous clay (bed 11) through marl to the limestone, which has become greatly modified by solution. Today, the marl and limestone lithologies do not form discrete beds. Sequences of marl through to limestone occur in several parts of the 'Fluvio-marine series' in the Isle of Wight (see Insole 1972) and some may be comparable. That solution must almost certainly have occurred is indicated by the abundance in the marl of oncolith-enclosed gastropods, *Bembridgia* opercula, slug plates and vertebrate remains, especially mammals, all of which have been encountered more sparsely in the soft limestone.

Keeping (1912: 131) noted that 'there is everywhere evidence of great disturbance of the strata, whether we refer this chiefly to large movements of faulting and overthrust, or the more superficial action of landslips, soil creep etc. The result has been a kneading up together of various deposits, so as to produce in many parts a mass much resembling some boulder clays'. In the recent excavations this statement is supported not only by the jumbled nature of the various limestone blocks embedded in the buff marl but also by a detached lobe of the manganiferous clay enclosed within the buff marl in the SW corner of Hole 5. Evidence for bedding is notably lacking. It is quite likely that the disturbance and solution features could have resulted from permafrost and solifluction activity during the Pleistocene.

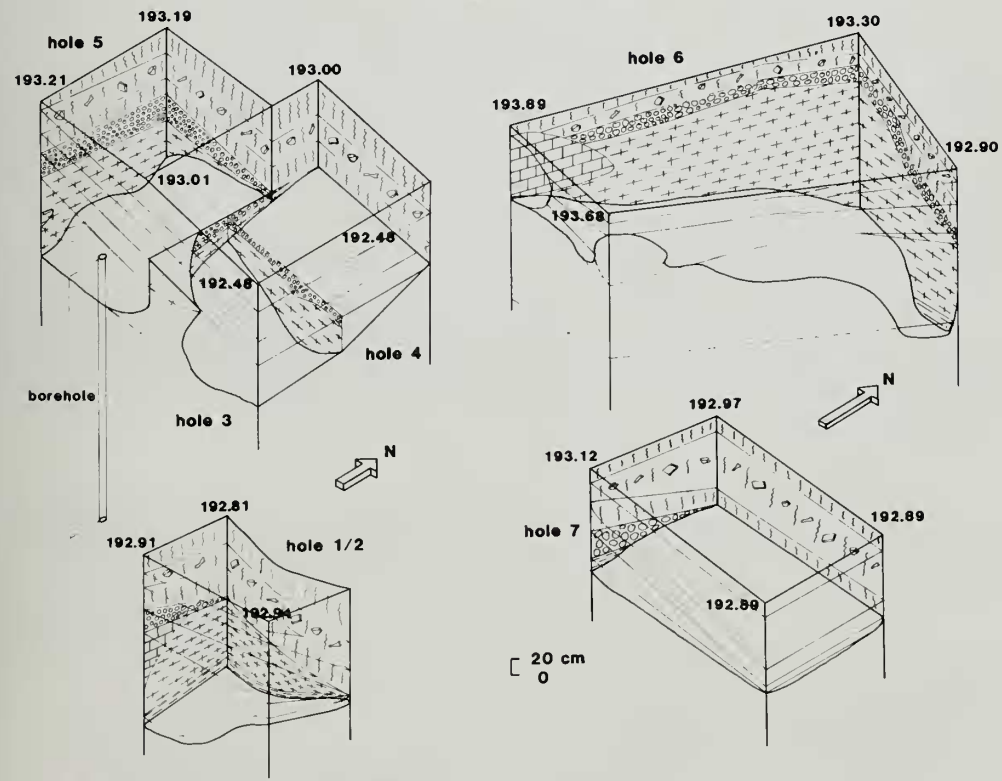
Beds 1–11. These all consist of manganiferous, very poorly sorted clay/silt/sand in which the grains are subangular to subrounded and up to 1 mm in diameter (see Text-fig. 5).

Bed 11: pale brown sandy silty clay with occasional angular fragments of flint. This formed the floor of the excavations, in which it was exposed in places. It also occurred in the top metre of the shallow hand-cored borehole put down from the floor of Hole 5. Beds 1–10 were exposed only in this shallow borehole.
Bed 10: pale brown clayey silty sand.
Bed 9: pale brown very sandy silty clay.
Bed 8: pale grey silty clay with low sand content.
Bed 7: pale brown very sandy silty clay.
Bed 6: pale grey very silty clay with low sand content.
Bed 5: pale grey sandy silty clay.
Bed 4: pale brown slightly clayey silty sand, the clay content reducing considerably in middle of bed.
Bed 3: pale brown very clayey silty sand.
Bed 2: very pale grey calcareous silty sand.
Bed 1: whitish buff very calcareous silty sand with small ovoid and tubular calcareous concretionary bodies (? oncoliths) 2–5 mm in diameter.

The base of the hand-cored borehole was at 187·8 m OD. After an unrecorded interval of 3·9 m, at 183·9 m OD is the top of an English China Clays (E.C.C.) borehole which was put down in 1973 at SY 92138 82367 and penetrated 72·2 m of sediment, the base being at 111·7 m OD. The recovery was very incomplete but the lithology was recorded as mainly hard sand or loamy sand, with frequent layers of flints which finally caused the drilling rods to jam and twist off before the pipe clays were reached. At about 150 ft down (138 m OD) a different lithology was

recorded, described as 'almost white silty clay w. brown yellow mottle and veining throughout'. This might represent the brick clay, exposed in Mr Bond's brickyard; but this stratum was recorded by Arkell (1947) as occurring from 20–80 ft below the limestone. There are many inconsistencies and gaps in our knowledge concerning the strata below the limestone and detailed logging of these would be a worthwhile future project. I am very grateful to English China Clays for allowing me to consult and reproduce data from their borehole log of Creechbarrow.

The Superficial Deposits. Bed A is very variable in thickness and probably resulted from weathering of the limestone, perhaps once naturally exposed at the surface. Hudleston (1902*a*: 250) surmised that a limestone needle was once exposed at the summit of the hill and later artificially levelled to produce limestone rubble (= bed A herein). If so, then the fine sandy soil of bed B was the natural soil formed subsequent to the building of a 'lodge' of which only the foundations now remain. This homogeneous horizon is devoid of human debris and wedges out rapidly westwards and summitwards in Hole 6. Hudleston (1902*a*: 253) later contradicted his own surmise when he suggested rapid disintegration of the limestone 'when exposed to the atmosphere' as the only explanation for absence of fragments on the flanks of the hill and its lack of use as a building stone. It seems more likely, therefore, that bed B was the natural soil formed before human occupation. Bed C was found to contain fragments of limestone, pottery, glass and roofing 'slate' (composed of Purbeck limestone) and a human phalangeal bone, as well as numerous black (? burnt) patches. This could have formed during occupation and/demolition of the 'lodge'. Bed D, the modern topsoil, has presumably developed since demolition, which, according to Hudleston (1902*b*), took place in the mid 18th Century.



Text-figure 6 Three-dimensional diagrams of stratigraphy in Creechbarrow holes 1–7. For lithological explanation see Text-figs 2, 5 and text. Figures are spot heights O.D. in metres of corners of holes measured from trigonometrical point. The floors of the excavations are shown blank.

Fragments of soft red limestone, perhaps representing Keeping's (1910: 437) 'Cherry Marl' (a workmen's term, given informal bed status by Cooper, 1976: 9), were found in bed C. Evidence of probable burning in bed C, the omission of any mention of the bed in Keeping's (1912: 130–131) or Hudleston's (1902*a*, *b*, 1903) detailed sections and its absence *in situ* in the sections exposed during the recent excavations all suggest that this rock has been discoloured by fire: a test, which involved burning a soft piece of Creechbarrow Limestone, produced a comparable red colour.

Structure. Hudleston (1902*a*: 249) calculated a dip of 10°–12° N for the Creechbarrow Limestone. Bloomfield (1913) showed similar dips for the underlying beds, but in this case apparently on the eastern side dipping westwards. Hudleston showed the limestone to continue some way down the northern slope of the hill and Arkell's (1947: 233) map reflects this. In the recent excavations, the base of the limestone appeared to rise at the northern end, the outcrop edge swinging sharply to the west, thus suggesting an east–west striking synclinal structure for the beds at the summit (Text-figs 4, 6). No excavations were made on the northern slope during the recent visits, only flint gravel being seen there in a long shallow trench which may be the remains of one of Hudleston's pits. It cannot be confirmed that limestone on the north face is *in situ*; but equally it cannot be affirmed that the dip of the beds in the recent excavations could not be due to recent earth movements (e.g. soil creep, solifluction, slumping due to mining of the pipe clay, etc.). Palaeogene sedimentology and structure of the whole area of the western Hampshire Basin (Wareham Basin) is the subject of a recent study by Plint (1981, unpublished Ph.D. thesis, Oxford), some aspects of which have been published (Plint 1982, 1983).

Systematic palaeontology

The taxa described are listed below with locality data (Table 1). The taxonomic order is essentially founded on Simpson (1945) but incorporating various subsequent modifications. Some of these are discussed under the relevant groups. Others concern the placing of Cetacea after Condylarthra from which they are considered to be derived (e.g. see Gingerich & Russell 1981); and the basic twofold division of Eutheria into 'insectivore-primate-rodent' and 'carnivore-ungulate' groups as advocated by Lillegraven (1969).

Dental nomenclature diagrams for various key groups explain the terms used in this work (Text-figs 8, 31, 43 and 54).

For mammalian ranges after the Bartonian, Ludian is used in preference to Priabonian and Stampian in preference to Rupelian, because of difficulties of correlation within each pair, in contrast to the relative ease of referring relevant European mammal faunas to the Ludian and Stampian. See Cavelier (1979) for information on correlating Ludian and Stampian with Priabonian and Rupelian.

See also the notes on taxonomic procedure, p. 195.

Table 1 The English Bartonian mammals and their localities: E – Elmore, H – Hengistbury, C – Creechbarrow, B – Barton, beds C–F. All are Class MAMMALIA Linnaeus, Subclass THERIA Parker & Haswell.

	Page	E H C B
Infraclass METATHERIA Huxley	215	
Superorder MARSUPIALIA Illiger, Order MARSUPICARNIVORA Ride	215	
Superfamily DIDELPHOIDEA Gray	215	
Family DIDELPHIDAE Gray	215	
Subfamily DIDELPHINAE Gray, Tribe DIDELPHINI Gray	215	
Genus *Amphiperatherium* Filhol	216	
1. *Amphiperatherium* aff. *goethei* Crochet	216	– – × –
2. *Amphiperatherium fontense* Crochet	220	– – × –

Table 1 (*continued*)

	Page	E H C B
Infraclass EUTHERIA Gill	222	
Order PROTEUTHERIA Romer	222	
Family PANTOLESTIDAE Cope	222	
3. ? Pantolestidae, gen. et sp. indet.	222	– – × –
Order LIPOTYPHLA Haeckel	223	
Suborder ERINACEOMORPHA Saban	223	
Family AMPHILEMURIDAE Heller	223	
Genus *Gesneropithex* Hürzeler	224	
4. *Gesneropithex figularis* sp. nov.	234	– – × –
Family NYCTITHERIIDAE Simpson	239	
Subfamily NYCTITHERIINAE Simpson	239	
Genus *Scraeva* Cray	240	
5. *Scraeva* sp. indet.	241	– – × –
Order CHIROPTERA Blumenbach	241	
Suborder MICROCHIROPTERA Dobson	241	
Family indet.	241	
6. gen. et sp. indet. 1	241	– – × ×
7. gen. et sp. indet. 2	243	– – × –
8. gen. et sp. indet. 3	245	– – × –
9. gen. et sp. indet. 4	245	– – × –
Order PRIMATES Linnaeus	245	
Suborder PROSIMII Illiger	245	
Infraorder TARSIIFORMES Gregory	245	
Family OMOMYIDAE Trouessart	245	
Subfamily MICROCHOERINAE Lydekker	245	
Genus *Nannopithex* Stehlin	249	
10. *Nannopithex quaylei* sp. nov.	249	– – × –
11. *Nannopithex* sp. 1	251	– – × –
Genus *Pseudoloris* Stehlin	252	
12. *Pseudoloris* cf. *crusafonti* Louis & Sudre	256	– – × –
Genus *Microchoerus* Wood	257	
13. *Microchoerus wardi* sp. nov.	259	– – × –
14. *Microchoerus creechbarrowensis* sp. nov.	261	– – × –
Infraorder LEMURIFORMES Gregory	267	
Family ADAPIDAE Trouessart	267	
Subfamily ADAPINAE Trouessart	267	
Genus *Europolemur* Weigelt	267	
15. *Europolemur collinsonae* sp. nov.	270	– – × –
Genus *Leptadapis* Gervais	274	
16. *Leptadapis* aff. *magnus* (Filhol)	278	– – × –
17. Adapinae, gen. et sp. indet.	282	– – × –
Order RODENTIA Bowdich	282	
Suborder SCIUROGNATHI Tullberg	282	
Infraorder PROTROGOMORPHA Zittel	282	
Family PARAMYIDAE Miller & Gidley	282	
Subfamily MANITSHINAE Simpson	283	
Genus *Plesiarctomys* Bravard	283	
18. *Plesiarctomys curranti* sp. nov.	283	– – × –
19. *Plesiarctomys hurzeleri* Wood	288	– – × –
20. ? Manitshinae, gen. et sp. indet.	290	– – × –
Subfamily AILURAVINAE Michaux	291	
Genus *Ailuravus* Rütimeyer	291	
21. *Ailuravus stehlinschaubi* Wood	293	– – × –

Table 1 (*continued*)

Table 1 (*continued*)

	Page	E H C B
Infraorder uncertain, Superfamily THERIDOMYOIDEA Alston	295	
Family PSEUDOSCIURIDAE Zittel	298	
Genus *Sciuroides* Major	300	
22. *Sciuroides rissonei* sp. nov.	301	– – × –
Genus *Treposciurus* Schmidt-Kittler	307	
Treposciurus helveticus Schmidt-Kittler	308	
Treposciurus helveticus helveticus Schmidt-Kittler	308	
23. *Treposciurus helveticus preecei* subsp. nov.	309	– – × –
Genus *Suevosciurus* Dehm	315	
24. *Suevosciurus authodon* sp. nov.	315	– – × –
Order APATOTHERIA Scott & Jepsen	327	
Family APATEMYIDAE Matthew	327	
Genus *Heterohyus* Gervais	329	
25. *Heterohyus* cf. *sudrei* Sigé	330	– – × –
26. *Heterohyus* aff. *nanus* Teilhard	330	– – × –
27. *Heterohyus morinionensis* sp. nov.	331	– – × –
Heterohyus spp. indet.	334	– – × –
Order CARNIVORA Bowdich	336	
Superfamily MIACOIDEA Cope	336	
Family MIACIDAE Cope	336	
Subfamily MIACINAE Cope	336	
Genus *Miacis* Cope	336	
28. ? *Miacis* sp. indet.	336	– – × –
29. ? Miacinae, gen. et sp. indet.	338	– – × –
Order CONDYLARTHRA Cope	338	
Family PAROXYCLAENIDAE Weitzel	338	
Genus *Vulpavoides* Matthes	339	
30. *Vulpavoides cooperi* sp. nov.	340	– – × –
Order CETACEA Brisson	342	
Suborder ARCHAEOCETI Flower	342	
Family DORUDONTIDAE Miller	342	
Genus *Zygorhiza* True	342	
31. *Zygorhiza wanklyni* (Seeley)	342	– – – ×
Family BASILOSAURIDAE Cope	342	
Genus *Basilosaurus* Harlan	342	
32. *Basilosaurus* sp. indet.	342	– – – ×
Order PERISSODACTYLA Owen	342	
Superfamily EQUOIDEA Hay	342	
Family PALAEOTHERIIDAE Bonaparte	342	
Genus *Propalaeotherium* Gervais	343	
33. *Propalaeotherium* aff. *parvulum* (Laurillard)	343	× – × –
Genus *Lophiotherium* Gervais	347	
34. *Lophiotherium siderolithicum* (Pictet)	347	– – × –
Genus *Plagiolophus* Pomel	353	
Plagiolophus curtisi sp. nov.	353	
35. *Plagiolophus curtisi curtisi* subsp. nov.	356	– – – ×
36. *Plagiolophus curtisi creechensis* subsp. nov.	364	– – × –
Genus *Palaeotherium* Cuvier	371	
37. *Palaeotherium* aff. ?*muehlbergi* Stehlin	371	– – – ×
38. *Palaeotherium* sp. indet.	373	× – – –
Suborder ANCYLOPODA Cope	374	
Family LOPHIODONTIDAE Gill	374	
Genus *Lophiodon* Cuvier	374	
39. *Lophiodon* cf. *cuvieri* Filhol	374	× – – –
40. *Lophiodon* cf. *lautricense* Noulet	376	– × – –

Table 1 (*continued*)

	Page	E H C B
Order ARTIODACTYLA Owen	376	
Suborder PALAEODONTA Matthew	376	
Superfamily DICHOBUNOIDEA Gill	376	
Family DICHOBUNIDAE Gill	376	
Genus *Hyperdichobune* Stehlin	376	
41. *Hyperdichobune* sp. 1	376	– – x –
42. ? *Hyperdichobune* sp. 2	379	– – x –
Family MIXTOTHERIIDAE Pearson	381	
Genus *Mixtotherium* Filhol	381	
43. *Mixtotherium* aff. *gresslyi* Rütimeyer	383	– – x –
44. ? *Mixtotherium* sp. indet.	389	– – x –
Family CEBOCHOERIDAE Lydekker	389	
Genus *Cebochoerus* Gervais	390	
45. *Cebochoerus minor* Gervais	391	– – – x
46. *Cebochoerusrobiacensis*Depéret	398	– – x –
Genus *Acotherulum* Gervais	399	
47. *Acotherulum campichii* (Pictet)	400	– – x –
Suborder ANCODONTA Matthew	404	
Superfamily ANTHRACOTHERIOIDEA Gill	404	
Family HAPLOBUNODONTIDAE Pilgrim	404	
Genus *Haplobunodon* Depéret	404	
48. *Haplobunodon venatorum* sp. nov.	404	– – x –
Family ? CHOEROPOTAMIDAE Owen	409	
Genus ? *Choeropotamus* Cuvier	409	
49. ? *Choeropotamus* sp. indet.	409	– – x –
Superfamily ANOPLOTHERIOIDEA Bonaparte	409	
Family ANOPLOTHERIIDAE Bonaparte	409	
Subfamily DACRYTHERIINAE Depéret	409	
Genus *Dacrytherium* Filhol	410	
50. *Dacrytherium elegans* (Filhol)	410	– – x –
Suborder TYLOPODA Illiger	412	
Superfamily XIPHODONTOIDEA Flower	412	
Family XIPHODONTIDAE Flower	412	
Genus *Dichodon* Owen	412	
51. *Dichodon* cf. *cervinus* (Owen)	413	– – x –
52. *Dichodon* sp. indet.	414	– – x –
53. Artiodactyla, fam., gen. et sp. indet.	414	– – x –

Class **MAMMALIA** Linnaeus 1758
Subclass **THERIA** Parker & Haswell 1897
Infraclass **METATHERIA** Huxley 1880
Superorder **MARSUPIALIA** Illiger 1811
Order **MARSUPICARNIVORA** Ride 1964
Superfamily **DIDELPHOIDEA** Gray 1827
(rank emend. Osborn 1910)

Family **DIDELPHIDAE** Gray 1827
Subfamily **DIDELPHINAE** Gray 1827
(rank emend. Simpson 1927)

Tribe **DIDELPHINI** Gray 1827
(rank emend. Crochet 1979)

TYPE GENUS. *Didelphis* L. 1758. Recent, North and South America.

INCLUDED GENERA. See Crochet (1979: 368) for long list of genera. The only two in the European Tertiary are *Peratherium* Aymard 1850 and *Amphiperatherium* Filhol 1879.

RANGE. Late Palaeocene to Eocene, Miocene to Recent, South America; early Eocene to early Miocene, Pleistocene to Recent, North America; and early Eocene to middle Miocene, Europe (from Crochet 1979).

DIAGNOSIS. See Crochet (1979: 368).

DENTAL NOMENCLATURE AND FORMULA. Dental nomenclature essentially follows the eutherian pattern (see Text-fig. 8, p. 222) with the exception of the five upper molar stylar cusps. These are lettered A to E (mesially to distally) and occupy the following positions of the eutherian stylar cusps: A (parastyle), B (stylocone), C (mesostyle), E (metastyle); D is between C and E (see Crochet 1980: fig. 2). Homologies are disputed (Clemens 1979: 200–201, fig. 11.1). Length and width measurements follow Clemens (1966: 4, text-fig. 1), with the addition of the length of the protocone lobe.

Crochet (1979, 1980) referred frequently to the length of the protofossa as an important character. This term equals the trigon basin (see Van Valen 1966: text-fig. 1; Szalay 1969: text-fig. 1), and is difficult to measure when worn. A more appropriate structure to describe the same character is the protocone lobe. This is the lingual section of the upper molar delimited buccally by the postflexus and may be what Crochet actually meant.

Numbering and naming of the cheek teeth is also disputed (see Clemens 1979: 202–203; Crochet 1980: 25–26). A conservative approach is adopted here, the four molariform teeth being referred to as $M\frac{1}{1}$–$\frac{4}{4}$.

Genus *AMPHIPERATHERIUM* Filhol 1879

(See Crochet 1980 for synonymy list)

TYPE SPECIES. *A. frequens* (Meyer 1846) Crochet 1977. Oligocene; Weissenau, West Germany.

INCLUDED SPECIES. *A. brabantense* Crochet 1979; *A. giselense* (Heller 1936) Crochet 1977; *A. bourdellense* Crochet 1979; *A. minutum* (Aymard 1846) Crochet 1977; *A. goethei* Crochet 1979; *A. lamandini* (Filhol 1876*b*) Crochet 1979; *A. maximum* Crochet 1979; *A. bastburgense* Crochet 1979; *A. fontense* Crochet 1979; *A. ambiguum* (Filhol 1877*b*) Crochet 1979; and *A. exile* (Gervais 1852) Crochet 1979.

RANGE. Early Eocene to middle Miocene, Europe.

DIAGNOSIS. See Crochet (1980: 59).

Amphiperatherium aff. *goethei* Crochet 1979

(Pl. 3, figs 1–6; Text-fig. 7A; Table 2)

v. *1977b Peratherium* sp. 1; Hooker: 141.
v. *1980 Amphiperatherium* sp. 1; Hooker & Insole: 37.

HOLOTYPE OF SPECIES. Left M^3 (UM Bux68.89). Middle Lutetian; Bouxwiller, Bas-Rhin, France.

RANGE OF SPECIES. Sparnacian to Lutetian, France.

DIAGNOSIS OF SPECIES. See Crochet (1979: 371)

MATERIAL. Right M^1 (M37110); left M^2 (M35631); right M^2 (M35632); left M^3 (M35633); two right M^3 protocone lobe fragments (M35634–5); right P_2 (M35636); left M_2 (M37112); left M_3 (M35637); left M_4 (M35638); left and right $M_{1/2/3}$ talonid fragments (M35642–3); right M_3 trigonid fragment (M35640); left M_4 trigonid fragment (M37113); two right M_4 trigonid fragments (M35641, M37114).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. M^1: The tooth has an oblique appearance caused by the mesially positioned protocone and acute distobuccal angle. Cusps B and D are subequal, C is slightly smaller and slightly nearer to D than to B. B is nearer to A than to C. The ectoflexus is moderately shallow and asymmetrical. The paracingulum narrows in front of the paracone. The protocone lobe is

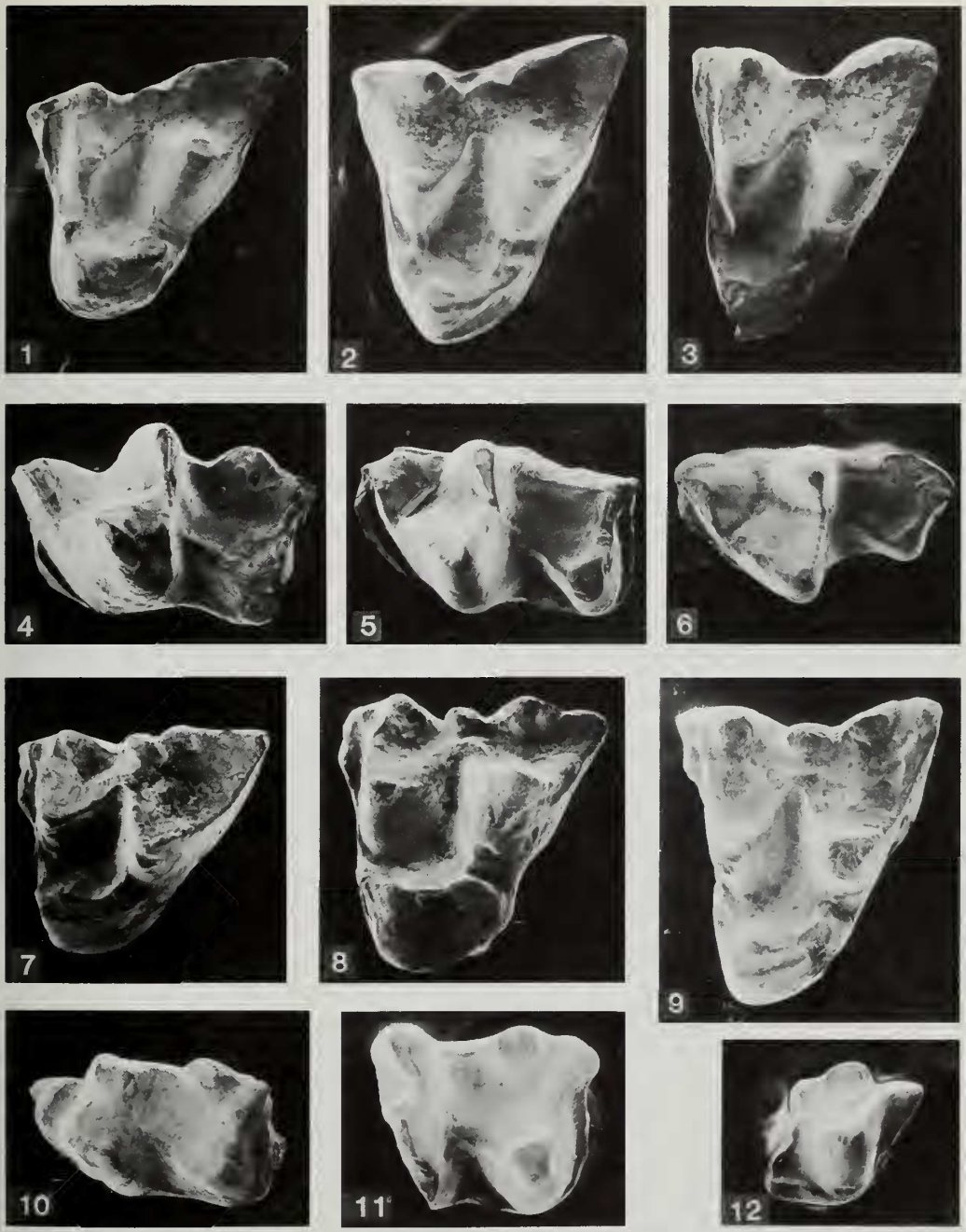


Plate 3 Scanning electron micrographs of occlusal views of molars of *Amphiperatherium* from Creechbarrow.

Figs 1–6 *Amphiperatherium* aff. *goethei* Crochet, ×24. Fig. 1, right M^1 (reversed) (M37110). Fig. 2, right M^2 (reversed) (M35632). Fig. 3, left M^3 (M35633). Fig. 4, left M_2 (M37112). Fig. 5, left M_3 (M35637). Fig. 6, left M_4 (M35638). See p. 216.

Figs 7–12 *Amphiperatherium fontense* Crochet, ×16. Fig. 7, left M^1 (M35390). Fig. 8, left M^2 (M35602). Fig. 9, right M^3 (reversed) (M37093). Fig. 10, left M_1 (M35612). Fig. 11, left $M_{2/3}$ with broken trigonid (M35391). Fig. 12, right M_4 talonid fragment (reversed) (M35617). See p. 220.

slightly abraded lingually and distally and it is not known whether it was rounded or angular lingually.

M^2: Cusps B and D are subequal, B being only very slightly larger. C is slightly smaller and significantly closer to D than to B. On M35632, B is equidistant between A and C, but on M35631 nearer to A and separated from C by a deep fissure. The ectoflexus is moderately shallow and asymmetrical. On M35632, the paracingulum narrows as on M^1 but insignificantly on M35631. The protocone lobe is angular lingually.

M^3: Cusps C and D are subequal and smaller than B. C is equidistant between B and D, and B is closer to A than to C. The ectoflexus is fairly deep and symmetrical. The paracingulum almost disappears in front of the paracone. The protocone is angular lingually.

On the three upper molar types represented, dilambdodonty is marked, narrowing the stylar shelf near cusp C so that it is less than half the width that it is at the metacone. The teeth are relatively short, probably in part due to the shortness of the metastylar wing. The protocone lobe is long relative to tooth length. The paraconule and metaconule are prominent, especially the latter; and so are the pre- and post-paraconule and premetaconule cristae.

M_2: The outline is relatively elongate (length about twice the width); and the lengths of trigonid and talonid are approximately equal. The protoconid is slightly mesial to the metaconid. The paraconid is about $\frac{3}{4}$ the height of the metaconid and their bases are of equal length. The entoconid is low and elongate oval in occlusal view. The postcristid is broken between the entoconid and hypoconulid. The hypoconulid is chipped and it is difficult to estimate its distal saliency. The slightly buccally concave cristid obliqua joins the protoconid midway between the buccal edge and the trigonid notch. The postmetacristid is restricted basally. The precingulid terminates at the protoconid.

M_3: Outline and trigonid/talonid proportions are as on M_2. The protoconid is exactly opposite the metaconid. The paraconid is about $\frac{3}{4}$ the height of the metaconid. The entoconid and hypoconulid are broken away. The cristid obliqua is more strongly concave buccally than in M_2 and joins the protoconid midway between the buccal and lingual tooth margins. The postmetacristid is restricted basally. The precingulid extends slightly round the protoconid and the ectocingulid bears a worn ectostylid.

M_4: The talonid is $\frac{3}{4}$ the width of the trigonid. The protoconid is exactly opposite the metaconid. The paraconid is $\frac{3}{4}$ the height of the metaconid and nearly twice as long basally; and the valley between is open. The entoconid and hypoconulid are chipped but the latter is closer to the former than to the hypoconid. The cristid obliqua has the same orientation and protoconid attachment position as on M_3. There is no postmetacristid. The precingulid terminates at the protoconid.

Measurements are given in Table 2.

Table 2 Tooth length (l) and width (w) and length of upper molar protocone lobe (lp) of *Amphiperatherium* aff. *goethei* and *A. fontense* from Creechbarrow. Measurements in millimetres.

Amphiperatherium aff. *goethei*

No.	Tooth	l	w	lp
M37110	M^1	1·63	1·70	0·90
M35631	M^2	1·75	2·02	1·00
M35632	M^2	1·72	1·88	1·05
M35633	M^3	1·53	1·93	0·90
M37112	M_2	1·88	1·17	–
M35637	M_3	(1·77)	1·18	–
M35640	M_3	–	1·17	–
M35638	M_4	1·77	1·15	–
M37113	M_4	–	0·97	–
M35641	M_4	–	1·00	–
M37114	M_4	–	1·00	–

Amphiperatherium fontense

No.	Tooth	l	w	lp
M35390	M^1	2·30	2·60	1·40
M37090	M^1	2·35	2·45	1·20
M37091	M^1	(2·50)	2·30	1·25
M35601	M^2	(2·60)	(2·65)	1·55
M35602	M^2	2·50	2·70	1·55
M35603	M^2	–	–	1·55
M35600	M^2	–	(2·30)	1·40+
M35604	M^2	2·55	2·75	1·45
M37092	M^2	(2·65)	(2·65)	1·60
M37093	M^3	2·50	2·80	1·35
M35612	M_1	2·35	1·30	–
M35396	M_1	–	1·15	–

AFFINITIES. Few specimens of different tooth types are available for one to judge intraspecific variation. However, the common occurrence of certain characters on different teeth, together with narrow size limits, points to the presence of an homogeneous assemblage. Both in size and morphology, this assemblage is closest to *A. goethei*, which is also defined on a relatively small sample. The principal differences from this species are as follows:

Upper molars with:	1. cusp C not doubled;
	2. slightly greater dilambdodonty;
	3. longer protocone lobe;
	4. stronger postparaconule and premetaconule cristae;
	5. slightly deeper M^1 ectoflexus.
Lower molars with:	6. slightly narrower outline;
	7. slightly higher paraconid;
	8. slightly buccally concave cristid obliqua.
Overall size:	9. slightly smaller (see Text-fig. 7A).

These differences, however, should not be overemphasized. A doubled cusp C is not constant in *A. goethei*; characters 2, 4 and 8 are very slight in degree; and 5 could well be within the range of intraspecific variation.

The stylar shelf in *A. goethei* was stated by Crochet (1979: 371, 1980: 89) to be normally developed, but, according to his figures, it differs little from that of *A. giselense*, which is stated (1980: 63) to be of reduced width. In *A.* aff. *goethei*, because of the slightly greater dilambdodonty, the stylar shelf adjacent to cusp C is even more reduced.

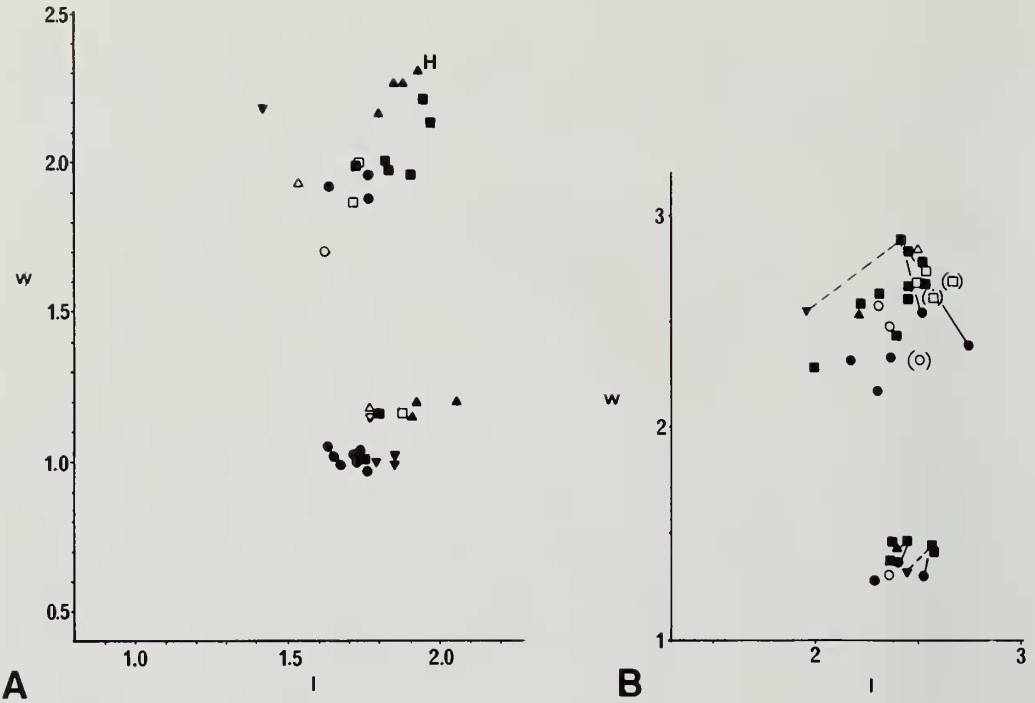
A. aff. *goethei* can be distinguished from the rather similar and highly variable but slightly smaller *A. minutum* by:

Upper molars with:	1. stronger cusp C;
	2. slightly greater dilambdodonty than even the most extreme variations of *A. minutum*;
	3. relatively shorter outline;
	4. relatively much longer protocone lobe;
	5. more prominent paraconule and metaconule and their cristae.
Lower molars with:	6. more mesial protoconid;
	7. lower entoconid;
	8. more lingual protoconid attachment of cristid obliqua;
	9. cristid obliqua slightly concave buccally;
	10. longer M_{1-3} talonids.

Crochet (1980: 79–88) documented a stratigraphical morphocline within *A. minutum*, ranging from late Bartonian to middle Oligocene. The earlier forms show the most differences from *A.* aff. *goethei* in character 2 and size. The later forms show the most differences from *A.* aff. *goethei* in characters 1 and 3.

The Creechbarrow assemblage shows no special similarity (except size) with the smaller of the two unnamed species of *Amphiperatherium* described from the Lower Headon Beds of Hordle Cliff by Cray (1973) as '*Peratherium* sp. A'. The latter has upper molars with much shallower ectoflexus, larger cusp C, slightly less dilambdodonty, broader paracingulum; and lower molars with relatively broader outline, shorter talonid, straight cristid obliqua, larger obliquely elongate entocristid, frequent postcristid between entoconid and hypoconulid and broader talonid on M_4.

Crochet (1980) considered *A. goethei* and *A. lamandini* to be closely related and to have an ancestor–descendant relationship. The youngest record of *A. goethei* is from the middle to late Lutetian, the oldest of *A. lamandini* late Ludian (with a doubtful record from the Marinesian of Grisolles). The Creechbarrow assemblage is stratigraphically intermediate between *A. goethei* and *A. lamandini*. In its differences 1, 3 and 7 from *A. goethei*, *A.* aff. *goethei* shows trends



Text-figure 7 Scatter diagrams of length (l) against width (w) of upper and lower molars of *Amphiperatherium*. In both diagrams the upper group of plots are upper, the lower group lower molars. ○ = $M\frac{1}{1}$; □ = $M\frac{2}{2}$; △ = $M\frac{3}{3}$; ▽ = $M\frac{4}{4}$. H = Holotype. Measurements in millimetres.

A. Solid symbols = *A. goethei* from Bouxwiller (H indicates holotype); hollow symbols = *A.* aff. *goethei* from Creechbarrow. Bouxwiller data are from Crochet (1980: fig. 104).

B. *A. fontense* from Fons 4 and La Bouffie (solid symbols) and Creechbarrow (hollow symbols). Associated teeth joined by solid and dotted lines belong to holotype from Fons 4. Fons 4 and La Bouffie data are from Crochet (1980: fig. 133).

towards *A. lamandini*, but not in the other characters. It is, however, difficult to evaluate all of these in terms of constancy, although at least some such characters as 6 and 8 appear to give more individuality to the Creechbarrow assemblage, in a direction different from that of *A. lamandini*. It may eventually be found that the Creechbarrow assemblage represents a new, possibly endemic, species, but it is here nomenclaturally linked with its closest relative.

Amphiperatherium fontense Crochet 1979
(Pl. 3, figs 7–12; Text-fig. 7B; Table 2)

v. *1977b Peratherium* sp. 2; Hooker: 141.
v. *1980 Amphiperatherium* sp. 2; Hooker & Insole: 37.

HOLOTYPE. Palate and mandible with upper and lower dentitions on both sides (UM F4-305). Upper Calcaire de Fons (early Ludian); Fons 4, Gard, France.

RANGE. Marinesian, England; Marinesian to early late Ludian, France; and early to early late Ludian, Switzerland.

MATERIAL. Two left P^3s (M36392, M36426); three left M^1s (M35390, M35608, M37090); right M^1 (M37091); three left M^2s (M35601–3); four right M^2s (M35600, M35604, M35606, M37092); three right M^3s (M35609, M37093–4); twelve $M^{1/2/3}$ fragments (M35607, M35610–1, M35630, M35713–4, M36395, M37095–8, M37111); right $P_{2/3}$ (M37099); left M_1 (M35612); right M_4 talonid fragment (M35617); fifteen $M_{1/2/3}$ talonid fragments (M35391, M35397–9, M35620–6, M37105–8) and twenty lower molar trigonid fragments (M35392–6, M35613–6, M35618–9, M35627–9, M37100–4, M37109).

DOUBTFULLY REFERRED SPECIMEN. Edentulous left mandibular fragment with distal M_4 alveolus (M37571).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. See Crochet (1979: 372).

DESCRIPTION. This species is much larger than and easily distinguished from *A.* aff *goethei* at Creechbarrow. Crochet (1980: 105–110) described French post-Bartonian assemblages in detail. Because of the apparent geographical and/or stratigraphical variation involved, variation in the Creechbarrow assemblage is documented here. Measurements are given in Tab. 2.

M^1: On two specimens, cusp C is quite large, only slightly smaller than, and well separated from, D. On two others (e.g. Pl. 3, fig. 7) it is slightly to much smaller, and very close to D. In the former there is little or no ectoflexus but it deepens asymmetrically with increasing reduction in size of cusp C. Cusp B is fairly constant in size, slightly larger than D, and in two specimens it has a strong distal crest (Pl. 3, fig. 7). Width of the stylar shelf at cusp C is fairly constant at about $\frac{1}{3}$ of its width at the metacone. There is a distinct postflexus in two out of three specimens and the protocone lobe is constantly angular lingually. The length of the protocone lobe varies from a little less to a little more than half the tooth length.

M^2: Cusp C remains in a central position but varies a little in size. B, C and D are subequal, although either B or D tends to dominate slightly. One fragmentary specimen (M35606) has a twinned cusp C, as often occurs in the probable ancestral species *A. bastburgense*. The depth of the ectoflexus varies from non-existent to shallow, depending on the size of cusp C. Two out of six specimens have a distal crest to cusp B (including M35606). The width of the stylar shelf is fairly constant and as on M^1. Presence and depth of a postflexus varies considerably and is most accentuated on M35602. Lingual angularity appears fairly constant as in M^1, although abrasion often makes it difficult to judge; it is reduced in the specimen with the longest protocone lobe (M37092). Length of the protocone lobe varies from about $\frac{1}{2}$ to $\frac{2}{3}$ of the tooth length.

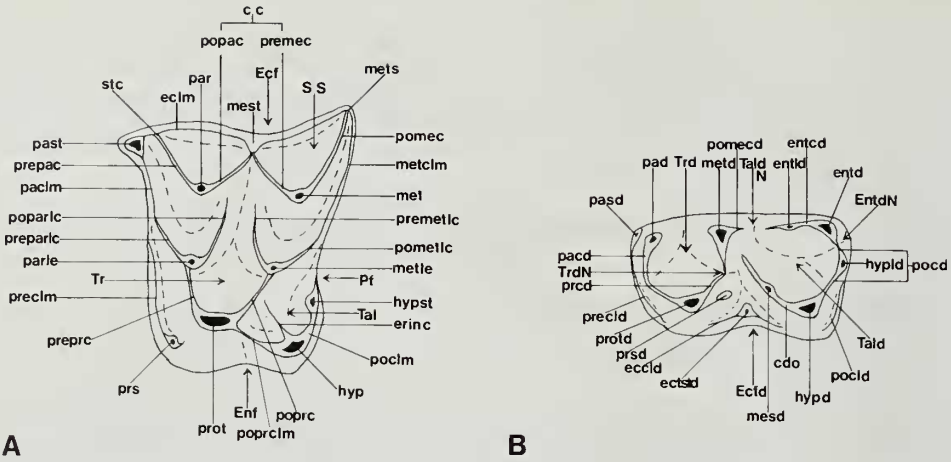
M^3: In M37093, regularly spaced cusps B, C and D decrease slightly in size in that order. A fragmentary specimen shows the same size relationship between C and D, but both are smaller than on M37093. In both the ectoflexus is shallow. Only M37093 is well enough preserved to show the other features (see Pl. 3, fig. 9).

M_1: The holotype M_1 is broken lingually but appears to have a slightly longer talonid relative to the trigonid than the only complete Creechbarrow lower molar (Pl. 3, fig. 10).

M_4: This talonid fragment is very narrow compared to the M_{1-3} talonids (Pl. 3, fig. 12).

Mandible: This edentulous fragment retains parts of the gently sloping leading edge of the ascending ramus, the inflected angular process and the large dental foramen typical of didelphids. Size suggests that it may belong to this species.

DISCUSSION. Of the characters which Crochet (1980: 109–110) found to vary between assemblages from the localities Fons 4 and La Bouffie on the one hand and Les Pradigues and Lavergne on the other, only one can be shown to be fairly constant at Creechbarrow, the lingual angularity of the upper molar protocone lobe. These results could be used to support either of his hypotheses: i.e. that the species is polytypic or that two parallel lineages developed (in the Ludian). The relatively small number of specimens from all localities suggests that the extent of the morphological intraspecific variation has not yet been adequately sampled.



Text-figure 8 Dental nomenclature of primitive eutherian quadritubercular cheek teeth. Based mainly on Van Valen (1966: text-fig. 1) and Szalay (1969: text-fig. 1). A, Left upper molar. Buccal edge towards top of page, lingual towards bottom. B, Left lower molar. Buccal edge towards bottom of page, lingual towards top.

Abbreviations:

A. cc—centrocrista
Ecf—ectoflexus
eclm—ectocingulum
Enf—entoflexus
erinc—'erinaceid crest'
hyp—hypocone
hypst—hypostyle
mest—mesostyle
met—metacone
metclm—metacingulum
metle—metaconule
mets—metastyle
paclm – paracingulum
par—paracone
parle—paraconule
past—parastyle
Pf—postflexus (new term)
poclm—postcingulum
pomec—postmetacrista
pometlc—postmetaconule crista
popac—postparacrista
poparlc—postparaconule crista
poprclm—postprotocingulum
poprc—postprotocrista
(=*Nannopithex* fold)
preclm—precingulum
premec—premetacrista
premetlc—premetaconule crista
prepac—preparacrista
preparlc—preparaconule crista
preprc—preprotocrista
prot—protocone
prs—protostyle
SS—stylar shelf
stc—stylocone
Tal—talon basin
Tr—trigon basin

B. cdo—cristid obliqua
eccld—ectocingulid
Ecfd—ectoflexid
ectstd—ectostylid
entcd—entocristid
entd—entoconid
EntdN—entoconid notch
entld—entoconulid
hypd—hypoconid
hypld—hypoconulid
mesd—mesoconid
metd—metaconid
pacd—paracristid
pad—paraconid
pasd—parastylid
pocd—postcristid
pocld—postcingulid
pomecd—postmetacristid
prcd—protocristid
precld—precingulid
protd—protoconid
prsd—protostylid
Tald—talonid basin
TaldN—talonid notch
Trd—trigonid basin
TrdN—trigonid notch

Infraclass **EUTHERIA** Gill 1872

Order **PROTEUTHERIA** Romer 1966 (*sensu* Sigé 1975)

Family **PANTOLESTIDAE** Cope 1884 (*sensu* Van Valen 1967)

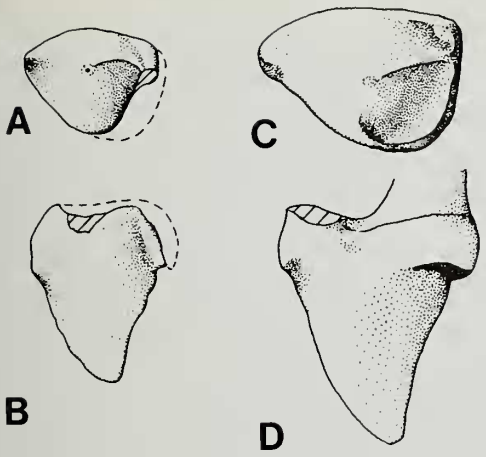
Cray (1973: 48) listed genera in this family up to that time. Subsequently Van Valen (1978) has synonymized *Pantomimus* with the arctocyonid condylarth *Prothryptacodon* and Heissig (1977) has synonymized *Opsiclaenodon* Butler 1947 and *Androconus* Quinet 1965 with *Cryptopithecus* Schlosser 1890. Further complications and problems with Palaeocene genera are discussed by Dorr (1977).

? **Pantolestidae**, gen. et sp. indet.
(Text-fig. 9A–B)

MATERIAL. Left $P^{1/2}$? fragment (M36435); two left $P^{2/3}$ fragments (M36390, M37407).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. $P^{1/2}$?: This single-cusped tooth, broken basally, is identified tentatively as it is smaller than those identified as $P^{2/3}$. Its curved cusp indicates it is not a lower tooth.



Text-figure 9 A–B, Pantolestidae indet. from Creechbarrow. Occlusal and buccal views respectively of left $P^{2/3}$ (M36390). C–D, *Cryptopithecus major* (Lydekker) from the Lower Headon Beds, Hordle Cliff. Occlusal and buccal views respectively of left $P^{2/3}$ (M34756). All × 8.

$P^{2/3}$: An upper tooth from Hordle Cliff (M34756; Text-fig. 9C–D) compares well in morphology with those of *Cryptopithecus sideroolithicus* Schlosser 1890, identified by Heissig (1977: 216, figs 6–8) as P^3 and P^4. It seems likely that the latter are really P^2 and P^3, as two teeth from Hordle Cliff, with morphology typical of that of a pantolestid P^4, are present in the BM(NH) collections. These are broader with a distinct protocone and are considered to belong to *Cryptopithecus major* (Lydekker 1887) Heissig 1977. Two teeth from Creechbarrow closely resemble M34756 but are slightly smaller. The better preserved (M36390) has a weaker parastyle which is situated higher on the crown and the preparacrista extends further apically. The distal and distolingual regions are missing in both teeth.

Order **LIPOTYPHLA** Haeckel 1866
(rank emend. Gregory 1910)

Insectivore classification has had a chequered history (see Butler 1972). Certain fossil and modern groups that at one time or another have been included peripherally in the Insectivora are generally now given ordinal status of their own (e.g. Apatotheria, p. 327, and Proteutheria, p. 222). For the rest Butler (1972) advocated the use of a restricted insectivore order, using Haeckel's (1866) name Lipotyphla, for the extant erinaceids, talpids, soricids, solenodontids, tenrecids and chrysochlorids and several extinct families. Novacek (1976) preferred to use the order Insectivora in a restricted sense for the Lipotyphla. The name Lipotyphla has the advantage of being narrower in its range of meaning than Insectivora. Butler (1972: 255) listed six important characters common to this group: 1, absence of caecum; 2, reduction of jugal; 3, expansion of maxilla in orbital wall, displacing palatine; 4, mobile proboscis moved by a series of muscles which influence the form of the skull; 5, reduced pubic symphysis; 6, haemochorial placenta. Characters 2–5 are the most likely to be useful in the fossil record and only 2–4 have been recognized in the early Tertiary. Moreover, skulls are rare and further extrapolation is by means of the teeth.

Suborder **ERINACEOMORPHA** Saban 1954 (*sensu* Sigé 1976)

Family **AMPHILEMURIDAE** Heller 1935

TYPE GENUS. *Amphilemur* Heller 1935 (including *Alsaticopithecus* Hürzeler 1947*b*). The synonymy of Russell *et al.* (1975) is upheld against Koenigswald & Storch's (1983) claimed distinctions between *Amphilemur* and *Alsaticopithecus*, which I cannot substantiate.

INCLUDED GENERA. *Gesneropithex* Hürzeler 1946 (including *Anchomomys* Stehlin 1916 in part) and *Pholidocercus* Koenigswald & Storch 1983.

RANGE. Lutetian to Ludian, Europe.

EMENDED DIAGNOSIS (modified from Koenigswald & Storch 1983). Dental formula $\frac{3\ 1\ 4\ 3}{3\ 1\ 4\ 3}$. $I\frac{1}{1}$–$P\frac{3}{3}$ of approximately equal size, although C^1 may be rather larger and P^1 rather smaller. Thus relatively little differentiation of the antemolar dentition, although sharp size and complexity change from $P\frac{3}{3}$ to $P\frac{4}{4}$. Lower teeth mesial to P_4 single-rooted and bladelike, and becoming progressively procumbent and overlapping forwards. $P\frac{4}{4}$ premolariform. P^4 essentially without metacone; *P_4 with* unicuspid talonid or with very small entoconid and *distinct cristid bisecting the distal protoconid slope and extending for the length of the talonid basin.* Molars relatively bunodont with rather inflated main cusps. $M\frac{1}{1}$ tend to be slightly longer than $M\frac{2}{2}$. *Upper molars with* buccal angles blunt, *a mesostyle at least on M^3*, narrow stylar shelves and well developed paraconule and metaconule with weak cristae. *M^{1-2}* quadrate, essentially as long as broad, *with postmetacrista short and weak*; *paracone and metacone* low and buccal and *better separated from each other than metacone and paracone of successive teeth*; hypocone medium to large, conical; erinaceid crest may be present. *Lower molars with* mesiodistally compressed trigonid, low transverse *paracristid* without paraconid *which does not reach lingual margin*; *broadly rounded talonid basin*; little height distinction between trigonid and talonid; talonid wider than trigonid at least on M_{1-2}; *hypoconid higher than entoconid*; cristid obliqua contacts distal trogonid wall below and buccal to the base of the protoconid–metaconid notch; entoconulid present; wear moderately transverse (*c.* 30°–40° to crown base) and normally penetrates no lower than buccal cingulum. *M_{1-2} hypoconulid* just lingual to midline, *separated from postcristid by distal grooves. Protoconid lower than metaconid on M_{2-3}*, subequal on M_1. *Mental foramina occur below P_2*, below P_4/M_1 and sometimes below P_3. Dermal ossification of tail known in one genus.

DISCUSSION. Koenigswald & Storch (1983) have recently provided compelling dental and postcranial evidence, from four skeletons of *Pholidocercus* from the Lutetian of Messel, W. Germany, which places this family in the Lipotyphla rather than the Primates, where it has frequently been classified in the past. I (Hooker 1982) independently came to the same conclusion, on the basis of cranial and dental remains of *Gesneropithex* from the Bartonian and Ludian of the Hampshire and Paris Basins. Koenigswald & Storch (1983) included in the family the poorly known type species of *Gesneropithex* but excluded other species that are referred to it herein. Inclusion of the latter, which considerably expand our knowledge of the genus, requires certain changes to the family diagnosis: e.g. size does not always decrease continuously from $M\frac{1}{1}$ to $M\frac{3}{3}$, one species showing much intraspecific size variation in $M\frac{3}{3}$. Those characters in the diagnosis which are italicized are unique to the Amphilemuridae and distinguish them from the other erinaceomorph families Adapisoricidae, Erinaceidae and Nyctitheriidae. Other characters distinguish them from only one or two of these families, but until the relationships within the Erinaceomorpha are better known the diagnosis cannot be made more precise. Comparison with the diagnosis of Russell *et al.* (1975) of the Adapisoricidae shows relatively few differences from that of the Amphilemuridae. In fact separation of the two leaves the Adapisoricidae based only on primitive characters. A possible solution to this problem may be a more detailed breakdown of the Adapisoricidae into smaller family units. This has already begun (Bown & Schankler 1982; Gingerich 1983, at subfamily level; Novack *et al.* 1985).

Genus *GESNEROPITHEX* Hürzeler 1946

TYPE SPECIES. *G. peyeri* Hürzeler 1946. Ludian fissure filling; Gösgen Pumpstation, Canton Solothurn, Switzerland.

INCLUDED SPECIES. *G. latidens* (Teilhard 1921) comb. nov.; *G. grisollensis* (Louis & Sudre 1975) comb. nov.; *G. figularis* sp. nov.; and *G.* sp. indet. (from Robiac; Sudre 1969*a*,*b*).

RANGE. Auversian to Ludian. England, France and Switzerland.

EMENDED DIAGNOSIS. Upper incisors, canine and $P^{1/2}$ with prominent distal cusp. Lower anterior teeth strongly procumbent. C_1 without talonid cusp. P^2 relatively narrow. P^3 with

small protocone and parastyle. P^4 approximately as long as broad with prominent parastyle. P_4 with subequal metaconid and protostylid both much smaller than protoconid; paraconid median. M^{1-2} essentially square in outline, hypocone as far from protocone as metacone is from paracone. Lower molars with paracristid far from lingual edge and without enamel wrinkling.

DIFFERENTIAL DIAGNOSIS. *Amphilemur* and *Pholidocercus* have the upper teeth in front of P^3 with weaker distal cusp; anterior premolars with lower length : width ratio; stronger upper molar mesostyles, M^{1-2} more trapezoidal with smaller hypocones closer to protocones; and P_4 without protostylid.

Amphilemur has P_4 with a larger metaconid and more lingual paracristid.

Pholidocercus has lower teeth in front of P_4 less procumbent; C_1 with talonid cusp; P^3 without paracone or parastyle; P^4 relatively shorter with smaller parastyle; P_4 with shorter talonid; and lower molars with paracristids extending further lingually and more concave talonid basins with enamel wrinkling.

Note that *Gesneropithex* and *Amphilemur* are known mainly from teeth and it is not known whether either were like *Pholidocercus* in the postcranial skeleton or presence of dermal ossification.

TAXONOMIC HISTORY. The treatment of species herein referred to *Gesneropithex* by authors is given below in chronological order. Koenigswald & Storch (1983) have comprehensively dealt with other members of the family in a similar way.

Teilhard (1921) described *Anchomomys latidens*, but the generic assignment was provisional. The adapid *Anchomomys* was then considered a tarsiid.

Hürzeler (1946, 1947*a*) described *Gesneropithex peyeri* as a primate in Prosimii, *incertae sedis.*

Simons (1962, 1963) and Crusafont-Pairo (1967) placed *Gesneropithex* in the Adapidae.

Russell *et al.* (1967: 40) placed *Gesneropithex* provisionally in the Adapidae.

Sudre (1969*a*) figured an M^1 and DP^4 from Robiac as *Dichobune* sp., an artiodactyl.

Sudre (1969*b*) figured a mandibular fragment with M_{2-3} from Robiac as *Gesneropithex* sp.

Szalay (1971*b*) considered *Gesneropithex* an adapisoricid.

Szalay (1974) considered '*Anchomomys*' *latidens* neither a close relative of *Anchomomys*, nor an adapid, nor a primate, but believed it to be an erinaceid insectivoran.

Russell *et al.* (1975) synonymized *Alsaticopithecus* with *Amphilemur*, placing it in the family Amphilemuridae as Primates *incertae sedis.* They also selected the mandibular fragment (NMB GP128) as lectotype of *Gesneropithex peyeri* which they considered was not an adapisoricid, but did not suggest what it could be. The paralectotype M^2 (NMB GP127) they reidentified as *Amphilemur* sp.

Louis & Sudre (1975) described a new species which they placed in '*Anchomomys*' ('*A.*' *grisollensis*) in ? Adapidae. They figured a probable DP^4 as a DP^3 and a DP^4 of *Microchoerus* or *Necrolemur* (cf. Schmidt-Kittler 1977*a*: fig. 10 for *Microchoerus* DP^4) as a DP^4 of '*A.*' *grisollensis.* They considered the new species related to '*A.*' *latidens*, neither being true *Anchomomys* and together probably with *A. pygmaeus* (Rütimeyer 1890) (now a *Periconodon*, see Gingerich, 1977*a*) belonging to a primate group of as yet uncertain affinities.

Hooker (1977*b*) recorded *Gesneropithex* from Creechbarrow.

Kay & Cartmill (1977: 36) showed that the interorbital index of 'the erinaceoid "*A.*" *latidens*' plotted well within the insectivores especially the tupaiids, but also alongside the microsyopid primate *Palaechthon.*

Sudre (1978*b*) reidentified the M^1 and DP^4, previously (1969*a*) identified as *Dichobune* sp., as *Mouillacitherium* aff. *elegans*, another dichobunid artiodactyl.

Hooker & Insole (1980) reidentified the Creechbarrow *Gesneropithex* as *Amphilemur* sp. 1.

Koenigswald & Storch (1983) included *Gesneropithex peyeri* in the Amphilemuridae but excluded '*Anchomomys*' *grisollensis.*

RECENT CONTRIBUTIONS. Two recent contrasting classifications of *Gesneropithex* are those of Szalay (1971*b*) and Russell *et al.* (1975), who also discuss *Amphilemur* in the same context. New

material from Creechbarrow described here as *Gesneropithex figularis* and from Hordle Cliff identified here as *Gesneropithex* aff. *grisollensis* (Louis & Sudre 1975) has an important bearing on their contrasting views. In the light of this material, the views of Szalay and Russell *et al.* will be considered in detail.

Szalay's (1971*b*) reasons for removing *Gesneropithex* from the Primates and reclassifying it in the '*Adapisorex*-like erinaceotans' were:

1. Shallower mandible than any early Tertiary primate.
2. P_4 unique if primate – narrow crown, mesial position of paraconid and large talonid unlike any adapid, anaptomorphid, microchoerid or early cercopithecid. Total complex of characters in P_4 compatible with *Adapisorex gaudryi*.
3. Distal border of talonid of lower molars barely rounded, and postcristid between prominent entoconid and hypoconid nearly straight when viewed in horizontal plane.
4. Tiny, centrally placed (molar) hypoconulid is deep in groove between entoconid and hypoconid.
5. (Molar) trigonid relatively erect, unlike the slightly procumbent talonid (=trigonid?) of adapids, microchoerids or anaptomorphids.
6. Upper molar lacks parastyle and metastyle and the nature of the cuspidate hypocone indicates that the genus most likely does not share homologous advanced similarities with upper molars of early Tertiary primates.
7. $M^{2?}$ is similar in position and conformation of hypocone to such erinaceotans as *A. gaudryi*, *Macrocranion tupaiodon* and *Galerix exilis*.

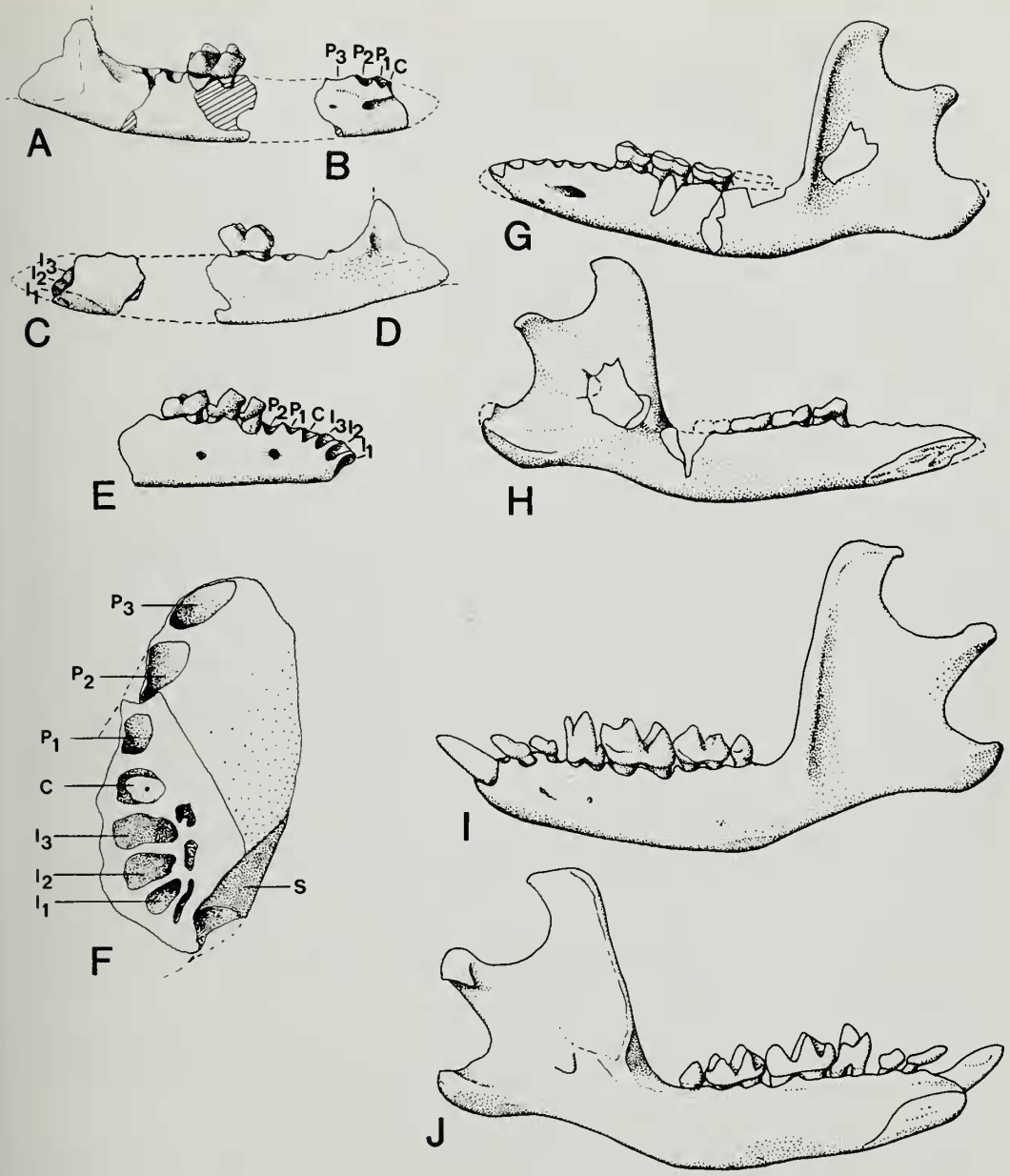
Russell *et al.* (1975: 171–172) admitted that *G. peyeri* P_4–M_2 showed many adapisoricid characters. They dismissed Szalay's (1971*b*) arguments for transfer of *Gesneropithex* to the erinaceoids by equating them with those that they used to return *Amphilemur* to the Primates. They (1975: 172) repeated some of the distinctions from the Adapisoricidae that they had already made for *Amphilemur* (1975: 170–171), but did not suggest relationships with this genus. They stated (1975: 171) that some specimens of the primates *Pelycodus*, *Hemiacodon* or *Omomys* have a mandible shallower than in *Amphilemur* (*Gesneropithex* has a mandible of similar depth). They suggested homologies for the four and a half alveoli mesial to P_4 which Szalay had ignored, and considered that the most mesial, also being the largest, had housed the canine and was thus unlike an adapisoricid. Koenigswald & Storch (1983: 473–474) reinterpreted these alveoli as single-rooted P_3–I_2.

Szalay's arguments were mainly concerned with removing *Gesneropithex* from the Primates, whereas the arguments of Russell *et al.* served only to remove it from the Adapisoricidae, without suggesting what it could be. The latters' reasons why *Amphilemur* was not an adapisoricid are of direct relevance and are listed below:

1. Either I_1 or lower canine missing makes the dentition atypical for the Adapisoricidae which have $\frac{2?1\,4\,3}{3\,1\,4\,3}$.
2. Molar paraconid only projects forwards a little on M_2, is central and closely hugs the metaconid.
3. Metaconid is high (compared to protoconid) on M_2.
4. Hypoconid instead of entoconid is highest of the talonid cusps.
5. P_4 and molars swollen and with broad talonid.

New discoveries. The new material provides an answer to two points raised above: the dental formula (point 1 of Russell *et al.* above), and the jaw depth (Szalay's point 1 above).

Dental formula. Two mandibular rami identified as *G.* aff. *grisollensis* from the Hordle Cliff Mammal Bed are complete to the very front. One shows seven alveoli in front of P_4; the other shows six alveoli in front of P_3 which itself has fused mesial and distal roots occupying a single alveolus (see Text-fig. 10E and G). The six teeth preserved in front of P_4 in *A. eocaenicus* are all single-rooted, and isolated teeth of almost identical morphology have also been recovered at Creechbarrow and from the Hordle Cliff Mammal Bed. Thus the most anterior alveolus in the



Text-figure 10 A–D, F, *Gesneropithex figularis* sp. nov. from Creechbarrow. A, D, lateral and medial views respectively of right posterior mandibular fragment with M_2 (M35407). B, C, F, lateral, medial and anteromedial views respectively of right anterior mandibular fragment (M37406). E, *Gesneropithex* aff. *grisollensis* (Louis & Sudre) from the Hordle Cliff Mammal Bed; lateral view of right mandibular fragment with P_3–M_1 (M50199). Alveoli are labelled; S = symphysis. G–H, lateral and medial views respectively of almost complete left mandibular ramus of *Gesneropithex* aff. *grisollensis* from the Hordle Cliff Mammal Bed (M50198). It shows P_4–M_2 and alveoli for I_1–P_3 and M_3. I–J, lateral and medial views respectively of left mandibular ramus of Recent hedgehog, *Erinaceus europaeus* Linné. A–E, G–J ×2; F ×6·6.

Hordle Cliff jaws must have contained an I_1. This conforms with Koenigswald & Storch's (1983) interpretation of *Amphilemur eocaenicus* as having possessed an I_1 and also the undoubted presence of this tooth in *Pholidocercus*. There is thus no support from the dental formula for reference of *Gesneropithex* to the Primates. The only primate with three incisors (*Purgatorius*) already shows some heterodonty here, unlike amphilemurids (Kielan-Jaworowska *et al.* 1979: 250). Several teeth from Creechbarrow closely resemble the tooth identified as I_2 (by comparison with the anteriormost tooth preserved in the jaw of *A. eocaenicus*) but differ in being broader and having a less oblique shape. These are herein tentatively identified as the elusive I_1. The Creechbarrow edentulous anterior mandibular fragment can be matched up with the Hordle Cliff jaws and the alveoli identified as I_1–P_3. Erosion at the front of the jaw means that only the deep recesses of the alveoli still remain (Text-fig. 10B, C and F).

Jaw depth. One of the two mandibular rami from Hordle Cliff mentioned above (M50198) is essentially complete (Text-fig. 10G–H). It was collected broken during sieving and skilfully mended by the collector Mr R. Gardner. P_4–M_2 are present but quite heavily worn. The horizontal ramus is shallow like *A. eocaenicus* and *G. peyeri* and the ascending ramus shows a striking resemblance to that of the modern hedgehog *Erinaceus europaeus* L. (see Text-fig. 10I–J). When tracings of the posterior horizontal and ascending rami of a range of early Tertiary and modern prosimian primates are superimposed on that of *G.* aff. *grisollensis*, with the bases of the tooth rows aligned, the primate ascending rami are not bent upwards and lie posterior and ventral to that of *Gesneropithex* (e.g. Text-fig. 11E). (Szalay & Delson's (1979: 50, fig. 17E–F) figure of a reconstructed *Palenochtha* jaw closely resembles an erinaceomorph in the characters mentioned above; however, study of the material of this genus in the UMMP shows it to be like other plesiadapiform primates and unlike erinaceomorphs.) The same is true for those prosimians with shallow as with deep jaws. It is probable that the rotation in primates was necessary to move the ascending rami backwards away from the enlarging eyes. The ascending ramus of most modern lipotyphlans and of known adapisoricids is like that of *Gesneropithex* in orientation. It is evident that the difference of opinion on jaw depth between Szalay (1971*b*) and Russell *et al.* (1975) is partly a question of definition. Although not necessarily shallower below the tooth row than in a primate, the upward bending of the ramus more posteriorly in *Gesneropithex* gives it a shallower appearance in this region, especially when the coronoid process is mainly broken away.

Thus both dental formula and jaw shape in *Gesneropithex* are dissimilar from primates and similar to adapisoricids. This supports Szalay's (1971*b*) conclusions and removes the first objection of Russell *et al.* (1975) to the inclusion of *Amphilemur* in the Adapisoricidae.

Other evidence. **Cranium.** An examination of the unique holotype cranium of *G. latidens* (MNHN Qu11012) from the Phosphorites du Quercy (exact horizon and locality unknown) provides further relevant characters (see Text-fig. 11A–C). The following are typical of lipotyphlans:

1. Extensive preorbital depression extending posteriorly right to orbit which has sharp laterally projecting anterior edge for accommodation and attachment of nasolabial muscles (see Butler 1956).
2. Lacrymal foramen inside orbit (as in *Macrocranion*, see Maier, 1979: 43).
3. When the complete mandibular ramus of *G.* aff. *grisollensis* from Hordle Cliff is occluded with the cranium of *G. latidens* (the two are very closely related if not conspecific) the distance between the anterior edges of the orbit and the ascending ramus leaves room for only a small eye.

In addition, the infraorbital foramen is large. This excludes most primates except for the earliest genus known from cranial remains – *Palaechthon* (see Kay & Cartmill 1977), where the infraorbital foramen is also large. There are, however, no other special similarities between *Gesneropithex* and *Palaechthon*.

Some striking similarities can, however, be observed between *Gesneropithex* and the modern galericine erinaceids *Hylomys*, *Neotetracus* and *Podogymnura*. In these genera and in tupaiids, however, the position of the orbit and infraorbital foramen vary considerably (see Table 3).

Table 3 Variation in position of orbit and infraorbital foramen in *Gesneropithex latidens* and other species.

Species	Position of infraorbital foramen	Position of anterior orbital edge
Gesneropithex latidens	P^4 middle	M^2 paracone
Macrocranion tupaiodon	P^3 distal edge	M^2 paracone
Palaechthon nacimienti	P^3 middle	M^1 paracone
Hylomys suillus	P^4 parastyle	M^1 paracone
Neotetracus sinensis	P^4 parastyle	M^1 paracone
Podogymnura truei	M^1 middle	M^2 paracone
Echinosorex gymnurus	P^4/M^1 junction	M^1 distal half
Tupaia glis	P^3 distal edge	M^1 mesial edge
Anathana elliotti	P^2 distal edge	P^4 parastyle
Urogale cylindrura	P^3 middle	M^2 middle
Dendrogale melanura	P^3 middle	M^1 middle
Ptilocercus lowi	P^4 middle	P^4 middle

Hylomys, *Neotetracus* and *Podogymnura* have a depression for the nasolabial muscles but only in *Hylomys* and *Neotetracus* has this a dorsal limiting ridge as in *Gesneropithex*. The orbit, as reconstructed in Text-fig. 11B, is more like *Podogymnura* than the other genera in position, size and apparent weakness of the dorsal edge. The irregular grooves on the frontal region of *Gesneropithex* are very similar in scale and pattern to *Neotetracus* and *Hylomys*; in contrast they are more anastomosing in *Podogymnura*.

The unique cranium of *G. latidens* is considerably distorted. It has been shortened, with the anterior region of the parietals having been sheared to form an imbricate structure. The right frontal has also been pushed anteroventrally to slide beneath the dorsal edge of the right maxilla, reducing the angle between the two, reducing the overall height of the cranium in this region and further shortening the whole cranium. In the reconstruction of the skull of *Gesneropithex*, an attempt has been made to reverse these processes. It is probable that the structural displacements which have taken place diagenetically were at sutures. The only ones visible on the specimen are those delimiting part of the lacrymal and maxilla (Text-fig. 11C). There is no suggestion of a jugal having a facial or orbital extension. The absence of this extension is a diagnostic lipotyphlan character but although the jugal has a facial extension in the tupaiids (Order Scandentia), the sutures are often completely fused and invisible. Maier (1979: 43) stated that in *Macrocranion* 'a slender process of the zygomatic (= jugal) forms the lower border of the orbit nearly reaching the lacrimal region; this is a feature more typical of the menotyphlan insectivores than of lipotyphla'; but the suture is not obvious from his figure (1979: 44, fig. 4).

The orbit of *G. latidens*, now mainly cleaned of matrix by Dr D. E. Russell, shows the presence of a lacrymal foramen and below it the much larger opening of the infraorbital canal; the arrangement is most like *Podogymnura* (see Text-fig. 11C–D) among modern galericines. See also Butler (1956: fig. 7) for orbital bones of *Echinosorex* and contrasting insectivores.

The back of the cranium has a prominent occipital crest, unlike *Hylomys*, *Neotetracus* or *Podogymnura* but more like the larger *Echinosorex* (Text-fig. 11A–B).

Teeth. The most relevant features of the teeth in the Amphilemuridae are compared with the early Tertiary prosimians and the Adapisoricidae in Table 4. They further support Szalay's (1971*b*) views on the erinaceoid relationships of *Gesneropithex* and indicate that the Amphilemuridae should not be included in the Order Primates.

The characters 2–5 of Russell *et al.* (1975), listed on p. 226 as reasons why *Amphilemur* is not an adapisoricid, will now be considered. The P_4 and lower molars seem to be no more swollen and to have talenids no broader than those of some adapisoricids. The reduction of the lower molar paracristid (paraconid absent) is associated with increase in size of the upper molar

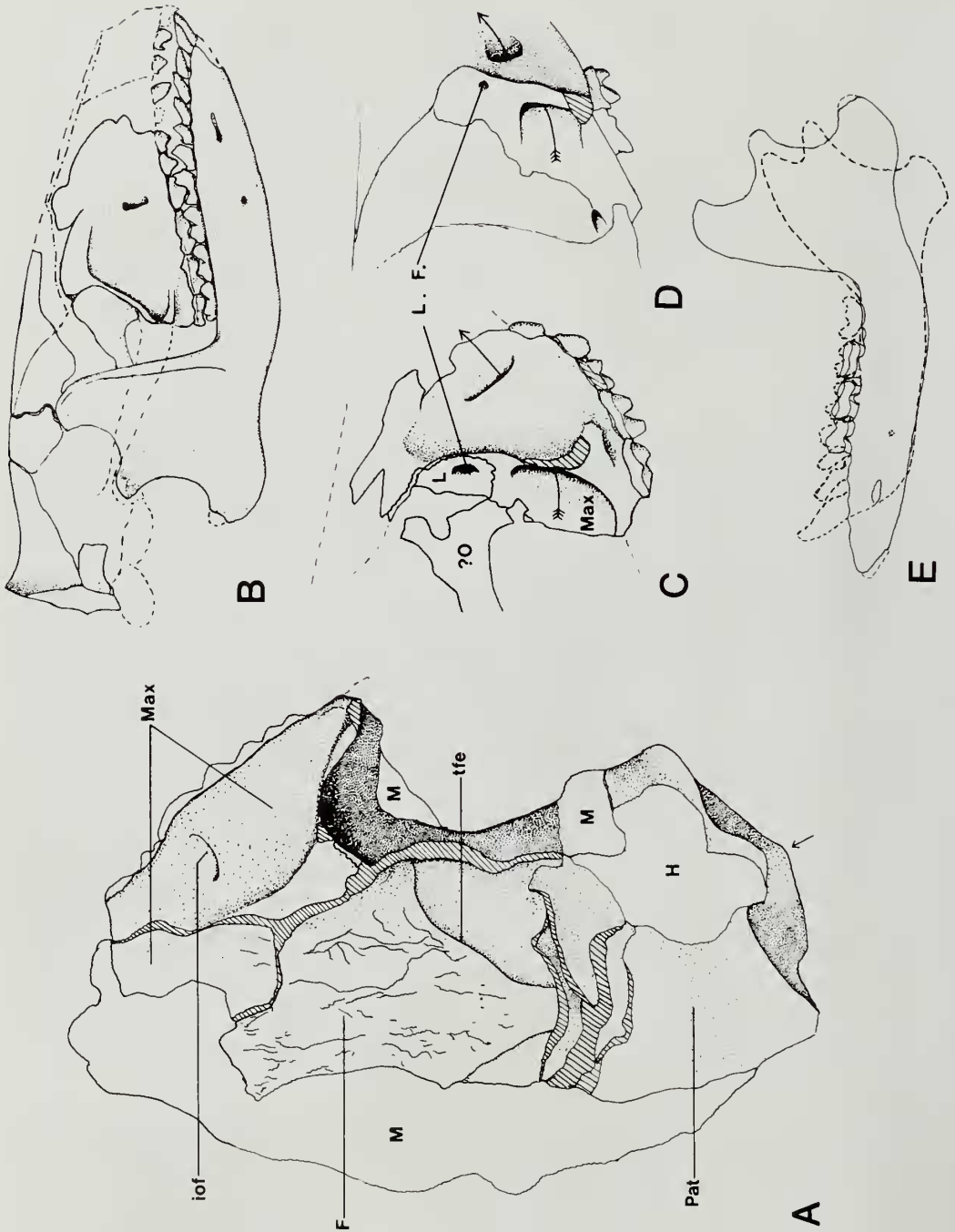

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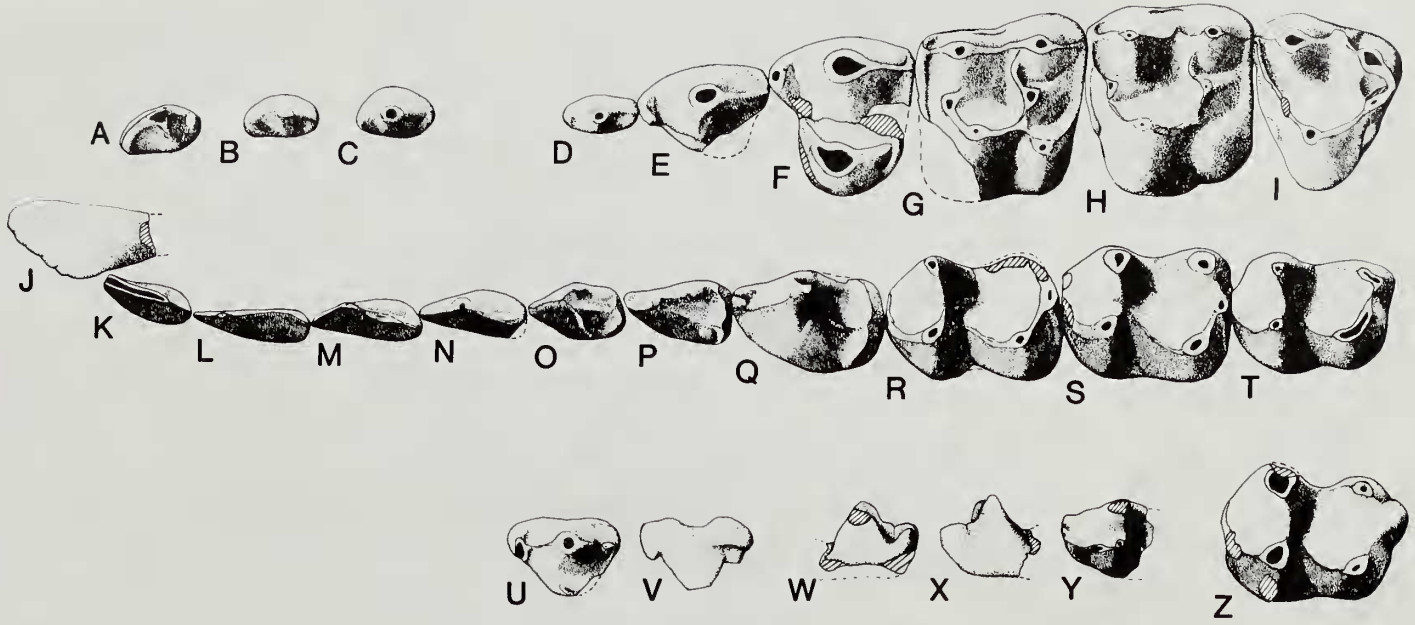
Table 4 Features of the teeth of Amphilemuridae compared with early Tertiary prosimians and Adapisoricidae.

Character	Early Tertiary prosimians	Amphilemuridae	Adapisoricidae
Tendency to develop *Nannopithex* fold	yes	no	no
Tendency to develop 'erinaceid' crest	no	yes	yes
M_3 talonid and hypoconulid	expanded	reduced	reduced
Presence of molar paraconid	yes	no	sometimes
Position of molar protoconid re metaconid	mesiobuccal	buccal	buccal on M_{2-3} mesiobuccal on M_1
Anterior lower teeth	heterodont, canine or incisor enlarged, other teeth upright or, if procumbent, broad	homodont, procumbent, blade-like	homodont, procumbent, blade-like where known (e.g. *Macrocranion*, see Tobien 1962; *Litolestes*, see Schwartz & Krishtalka 1976)

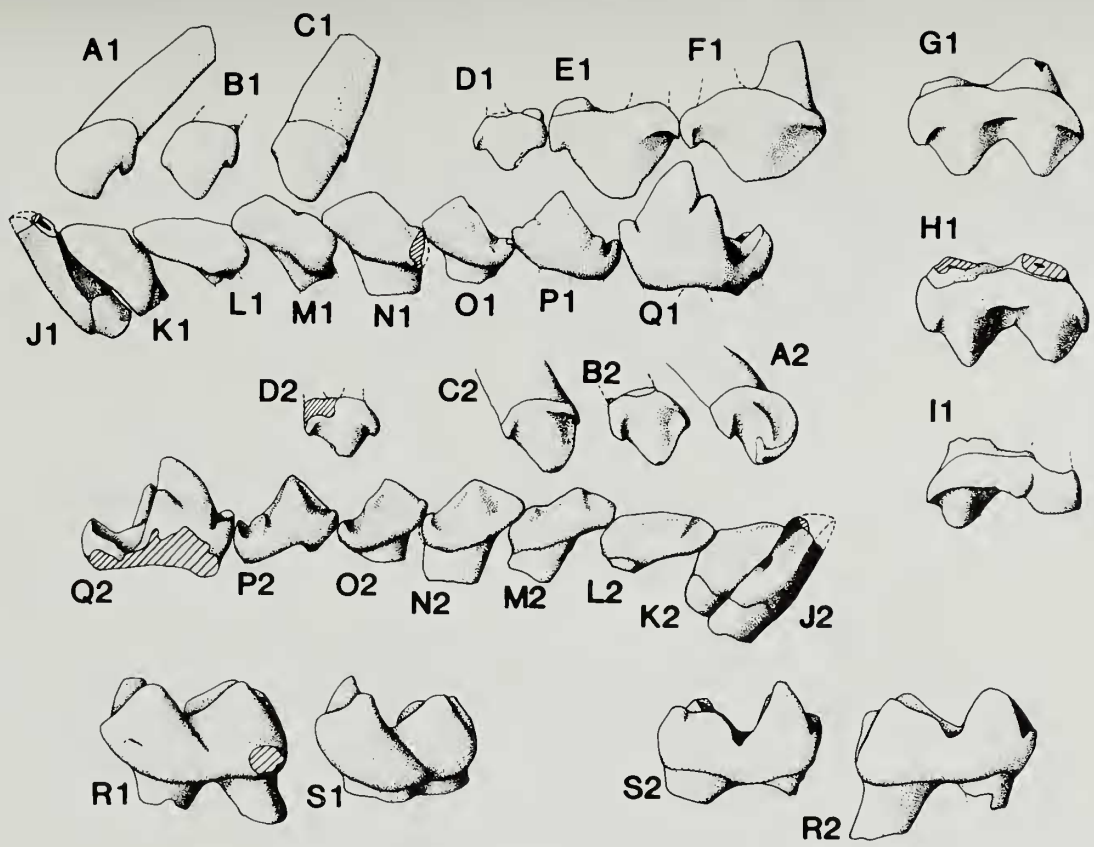
hypocone and more transverse shear between the teeth. The increase in height of the lower molar hypoconid is associated with the greater separation of the upper molar paracone and metacone. The lower molar metaconid is the same height as the entoconid as in adapisoricids; therefore the protoconid must have reduced in size. This is likely to be related to the reduction of the upper molar metastyle causing the metacone of one tooth to lie nearer to the paracone of the following tooth. These modifications are typical of mammals whose teeth have attained the quadritubercular state, as for instance has happened independently in ungulates and primates. Most of the other characters of *Amphilemur* and *Gesneropithex* link them strongly with the Adapisoricidae. Those that do not, instead of pointing to relationships with primates, suggest modifications for a less insectivorous, more herbivorous diet, as has already been suggested for *Macrocranion*, a closely related adapisoricid (see Maier 1979).

A possible ancestry of the Amphilemuridae could be sought among the pre-Middle Eocene Adapisoricidae. *Neomatronella* from the European early Eocene is a potential candidate. It shows certain characters in common with the Amphilemuridae like a similarly reduced M_3 talonid; lower molar paracristid not reaching lingual edge; M_{1-2} hypoconulid distinctly

Text-figure 11 A, dorsal view of holotype cranium of *Gesneropithex latidens* (Teilhard) (MNHN Qu11012) from the Phosphorites du Quercy; ×3·3. Abbreviations: M = matrix; H = hole; F = frontal; iof = infraorbital foramen; Max = maxilla; Pat = parietal; tfe = edge of temporal fossa; L = lacrymal; O = orbitosphenoid. Oblique hatching indicates broken surface of bone and arrow the position and orientation of midline of posterior region of cranium. B, reconstruction of *Gesneropithex* skull, based on holotype cranium of *G. latidens* (MNHN Qu11012) and left (reversed) mandibular ramus (M50198) from Hordle Cliff, with addition of teeth of *G. figularis* sp. nov. from Creechbarrow; ×2. C–D, posterolateral views of right orbital regions of crania of *Gesneropithex latidens* (holotype) and Recent *Podogymnura truei* Mearns (BMNH ZD53.660) respectively; ×3·3. L.F. = lacrymal foramen; arrow indicates course of infraorbital canal. E, outlines of mandibular rami of *Gesneropithex* aff. *grisollensis* (Louis & Sudre) (unbroken line) ×2, and of *Pseudoloris parvulus* (Filhol) (broken line) about ×4, superimposed with the cheek tooth rows aligned. *G.* aff. *grisollensis* is based on a specimen from Hordle Cliff (M50198), and *P. parvulus* both on a specimen from Hordle Cliff (M50200) and on MNHN unnumbered from the Phosphorites du Quercy.



Text-figure 12 *Gesneropithex figularis* sp. nov., from Creechbarrow. A–U, Y–Z are occlusal views, V and X buccal views and W lingual view; all × 5·5. A, right I^2? (reversed) (M36227). B, right I^3? (reversed) (M37142). C, left upper canine (M37403). D, left $P^{1/2}$ (M37141). E, left P^3 (M36417). F, left P^4 (M35653). G, right M^1 (reversed) (M35654). H, **holotype** right M^2 (reversed) (M35420). I, left M^3 (M35659). J, left i_1? (M37139). K, right I_2 (reversed) (M35663). L, right I_3 (reversed) (M35666). M, right lower canine (reversed) (M35668). N, left P_1 (M35670). O, left P_2 (M35402). P, left P_3 (M35678). Q, right P_4 (reversed) (M35681). R, left M_1 (M35685). S, right M_2 (reversed) (M35683). T, right M_3 (reversed) (M35410). U–V, right DP^3? (reversed) (M37405). W–Y, right DP_4 (reversed) (M35684). Z, right M_3 (reversed) (M37130).



Text-figure 13 *Gesneropithex figularis* sp. nov., from Creechbarrow. A1–S1 are buccal views, A2–D2, J2–S2 lingual views, all ×5·5. A, right I^2? (reversed) (M36227). B, right I^3? (reversed) (M37142). C, left upper canine (M37403). D, left $P^{1/2}$ (M37141). E, left P^3 (M36417). F, left P^4 (M35653). G, right M^1 (reversed) (M35654). H, **holotype** right M^2 (reversed) (M35420). I, left M^3 (M35659). J, left I_1? (M35660). K, right I_2 (reversed) (M35663). L, right I_3 (reversed) (M35666). M, right lower canine (reversed) (M35668). N, left P_1 (M35670). O, left P_2 (M35402). P, left P_3 (M35678). Q, right P_4 (reversed) (M35681). R, right M_2 (reversed) (M35683). S, right M_3 (reversed) (M35410).

separated from postcristid; and *Amphilemur*-like P_4. In other ways it is a typical adapisoricid but only teeth from $P\frac{4}{4} - M\frac{3}{3}$ are known (Russell *et al.* 1975).

Gesneropithex figularis sp. nov.
(Text-figs 10A–D, F, 12–14; Table 5)

v. *1977b Gesneropithex* sp.; Hooker: 141.
v. *1980 Amphilemur* sp. 1; Hooker & Insole: 37.

NAME. Latin, 'pertaining to a potter', referring to English China Clays (Wareham) Ltd., whose help and access to Creechbarrow is much appreciated.

HOLOTYPE. Right M^2, M35420.

PARATYPES (100). The edentulous mandibular fragments M35408, M35695 and M37406 and the teeth (one in a jaw fragment M35407) listed in Table 5.

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Large species of *Gesneropithex*, mean length of $M^2 = 3{\cdot}89$ mm (range 3·70–4·15 mm). M^1/P^4 area ratio = 1·29–1·65. M^1/M^2 length ratio = *c.* 1·0. M^2 length/width ratio = 0·87. $M^{1\ 2}$ mesostyle normally small to absent; ectocingulum weak; paraconule and metaconule cristae normally strong. P^4 without metacone. P^3 length 92–94% of P^4 length.

DIFFERENTIAL DIAGNOSIS. *G. grisollensis* is smaller, having a slightly stronger M^{1-2} ectocingulum and lower P^3/P^4 length ratio.

G. latidens is smaller, has a lower M^1/P^4 area ratio, higher M^1/M^2 length ratio, slightly stronger ectocingulum, small metacone on P^4 and lower P^3/P^4 length ratio.

G. peyeri is slightly smaller, M^2 length/width ratio lower, M^2 mesostyle large, M^2 ectocingulum slightly stronger and paraconule and metaconule cristae weak.

G. sp. indet. (Robiac; Sudre 1969*a*, *b*) may be slightly larger and has weak paraconule and metaconule cristae. See Text-fig. 14 for size comparisons.

DESCRIPTION. There are certain problems in attributing various anterior teeth to this genus and species. The I_2–P_4 have been identified by comparison with Heller (1935: pl. 1) and a cast of the syntype right mandibular ramus of *A. eocaenicus* (GH 7416); note that I_2 was apparently missing when Dr D. E. Russell cast this specimen, and none of the three syntype rami could be located in Halle in 1979. The attempted identification of I_1 has been explained above. Identification of upper teeth mesial to P^4 is more indirect. In the case of P^3 this was done by comparison with P^3 of the holotype of *G. latidens*. This cranium also has P^2, but the teeth from Creechbarrow which resemble P^2 are no larger than *G. latidens* P^2 and, in contrast, have a parastyle. Two likely possibilities are that mesial premolars are intra- or inter-specifically variable in size, or that these small P^2-like teeth are P^1s which resemble P^2 in morphology, or both. M37403 is identified as the upper canine by comparison with that tooth of *A. leemanni* (see Hürzeler, 1948*a*: 346, figs 2c, 3b, 4b). A possible upper incisor of *A. leemanni* was figured by Hürzeler (1948*a*: 346, figs 2d, 3c). The tooth which he figured (1948*a*: 351, figs 10c, 11c, 12c) as the lower canine contrasts strongly with the lower canine of *A. eocaenicus* in being less procumbent and having oblique wear extending down one side of the crown like the upper canine. It is also almost identical to the erupting right I^2 of *Pholidocercus* (Koenigswald & Storch 1983: fig. 19). It is tentatively identified as I^2 and Hürzeler's possible upper incisor as I^3. Koenigswald & Storch (1983: 472) identified these teeth as DP_1 and DP^1 respectively in *A. leemanni*. The lingual wear of the former, however, would make it an upper not a lower tooth.

No tooth has been recognized as a potential I^1, but four teeth from Creechbarrow have similar shape and wear to the *A. leemanni* $?I^2$. They differ in having a more bulbous lateral outline and a prominent ?metastyle. On one (M36227) a mesial interstitial facet suggests the presence of an I^1. The paracone forms a rib on the lingual wall and the wear facetting extends along this as well as on the ?metastyle and all along the mesial edge of the tooth, which forms a lingually salient ridge from the tip of the paracone to the crown base.

Table 5 Length (l) and mesial (w_1) and distal (w_2) width measurements of teeth of *Gesneropithex figularis* sp. nov. from Creechbarrow. M35420 (*) the holotype; all other specimens paratypes. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1	w_2
M36227	RI^2?	1·95	1·10	
M36226	LI^2?	1·80	1·10	
M36225	RI^2?	2·20	1·10	
M37404	RI^2?	(1·90)	(1·10)	
M37142	RI^3?	1·80	1·05	
M36793	LI^3?	2·00	1·20	
M37403	LC^1	1·75	1·15	
M37141	LP^2?	1·75	0·85	
M36442	LP^2?	1·60	1·00	
M35652	RDP^3?	2·55	–	
M35651	LDP^3?	(2·40)	–	
M37405	RDP^3?	2·50	1·80	
M36417	LP^3	3·05	–	
M37133	LP^4	3·25	–	
M35653	LP^4	3·30	3·70	
M36383	LP^4	–	–	
M35417	LM^1	3·85	(3·75)	
M35654	RM^1	3·90	3·90	
M35419	LM^1	–	4·00	
M37134	LM^1	3·80	–	
M35420*	RM^2	3·80	(4·40)	
M35418	LM^2	3·70	4·25	
M35655	LM^2	3·90	4·50	
M35657	RM^2	–	–	
M37135	LM^2	4·15	4·85	
M37136	RM^2	–	(4·30)	
M35658	LM^3	2·95	3·75	
M35656	LM^3	3·15	3·75	
M35659	LM^3	3·50	4·05	
M35660	LI_1?	–	1·25	
M37138	RI_1?	2·30	–	
M35661	LI_1?	–	1·35	
M37139	LI_1?	2·80	1·20	
M35663	RI_2	2·30	0·90	
M35662	LI_2	2·15	0·90	
M35664	RI_2?	–	1·15	
M35665	LI_3	(2·40)	1·00	
M35667	RI_3	–	(0·95)	
M35666	RI_3	2·60	0·80	
M35668	RC_1	2·55	1·00	
M35670	LP_1	(2·50)	1·10	
M37120	LP_1	2·60	1·30	
M35672	RP_1	2·25	1·10	
M35671	LP_1	2·30	1·05	
M35673	RP_1	2·85	1·00	
M37121	RP_1	2·20	1·00	
M35674	RP_1	–	–	
M35669	LP_1	2·20	1·10	
M35675	RP_1	2·65	1·30	
M35676	RP_2	2·40	1·25	

Table 5 continued

Table 5 Continued

No.	Tooth	l	w_1		w_2
M37123	LP_2	2·65		1·65	
M37122	LP_2	(2·90)		1·65	
M35403	RP_2	2·50		1·45	
M35404	RP_2	2·65		1·55	
M35402	LP_2	2·20		1·30	
M35677	LP_3	2·35		1·35	
M35678	LP_3	2·50		1·50	
M35684	RDP_4	–	1·85		–
M37124	LDP_4	–	1·65		–
M35681	RP_4	3·60		(2·15)	
M35680	LP_4	3·40		(1·85)	
M35679	LP_4	(3·30)		2·05	
M35682	RP_4	(3·70)		2·10	
M35405	RP_4	–		2·05	
M35406	RP_4	3·60		2·05	
M37125	LM_1	(3·75)	(2·85)		3·00
M35685	LM_1	4·00	2·80		(2·95)
M35407	RM_2 in jaw	4·55	3·10		3·40
M35683	RM_2	3·85	2·90		(3·10)
M35409	RM_2	4·40	3·55		3·45
M37126	RM_2	4·05	3·20		3·50
M37129	RM_3	–	–		–
M37128	LM_3	(4·00)	3·00		2·70
M37691	RM_3	–	–		2·55
M37690	LM_3	(3·75)	2·65		2·40
M35688	LM_3	3·85	3·15		2·75
M35689	RM_3	–	–		2·60
M35412	RM_3	–	2·50		2·30
M35410	RM_3	3·75	2·70		2·55
M35411	RM_3	–	–		2·90
M37130	RM_3	4·15	3·20		2·85

$?I^3$ is intermediate in morphology between I^2 and the upper canine. It has small ?parastyle, the mesial margin being less ridged, and a smaller ?metastyle. The distribution of facetting is similar to that of $?I^2$ but less extensive.

The upper canine differs from that of *A. leemanni* in having small ?parastyle and ?metastyle.

$P^{1/2}$ is smaller and lower-crowned than I^3 and has prominent parastyle and metastyle. *G. latidens* P^2 and *A. leemanni* $?P^1$ in contrast have no parastyle. There appears to have been a single root pinched in the middle. All the more mesial upper teeth are single-rooted with no sign of pinching, whilst all the more distal upper teeth have three roots.

P^3 has the protocone broken off but this cusp must have been much smaller than on P^4. Length of this tooth, however, is much closer to that of P^4 than it is in *G. latidens* or *G.* aff. *grisollensis*. The morphology is, however, quite similar.

Teeth differing from P^3 only in being smaller and having thinner enamel, a lower paracone, very small metacone on the postparacrista, larger parastyle and metastyle and very small protocone are identified as DP^3.

P^4: on M36383, the rather buccally orientated postprotocrista joins the distal cingulum, as on *G. grisollensis*; on M35653 it stops short and the distal cingulum extends more lingually as in *G. latidens*. There is no sign of a metacone, but a small cuspule occurs in M35653 and M37133 immediately mesial to the metastyle. A similar condition occurs in a P^4 of *G. grisollensis* from Grisolles where there also occurs a second more mesial cuspule which probably represents a metacone.

The morphology of the upper molars is essentially the same as in *G. grisollensis*. There is individual variation in the development of the pre- and post-paraconule cristae: one or other may be missing. There is also some overlap in the morphology of M^2 and M^3. For instance the M^2, M35655, has a distal interstitial facet, but has a relatively lingually tapering outline with smaller hypocone than usual and a large mesostyle like M^3. Conversely, the M^3, M35656, has no distal interstitial facet and is the correct size for M^3 (smaller than M^2), but has only a slightly lingually tapering outline and a large hypocone like M^2. These variations can most simply be explained by differing positions of the field of development of various characters with respect to the tooth (see Butler, 1939, 1967).

$?I_1$ differs from I_2 in being larger, the crown base being relatively broader, the mesial and distal edges flaring occlusally and the angle of the occlusal with the mesial edge being slightly less acute. The mesial interstitial facet is also longer and extends further down the crown, which on this side passes basally straight into the root without changing orientation. From the preserved I_1 alveoli on the two Hordle Cliff jaws, the tooth was just as procumbent as I_2 (cf. Heller 1935: pl. 1, figs 1a, b) but judged from the mesial interstitial facet must have been orientated more transversely in the jaw. M37139 is unworn and shows a faintly scalloped edge but is not deeply dissected like the lower incisors of the adapisoricid *Litolestes* (see Schwartz & Krishtalka, 1976). From overall size and the size and extent of the bevelled worn edges of M35660 and M35661, I^1 must have been at least as large as $?I^2$ and have occluded along the whole length of I_1. Whether or not there was an upper mesial diastema is not certain.

I_2 is much the same as in *A. eocaenicus*. The mesial and distal crown edges are parallel and the mesial one flares slightly mesially away from the root. The mesial interstitial facet is restricted to the occlusal end of the mesial crown margin and is parallel to the mesial edge of the root.

I_3 is blade-like, very procumbent, and mesially evenly tapering; the protoconid shows lingually as a rib but projects little if at all occlusally. The mesial interstitial facet is oblique immediately below the mesial end of the crown.

The lower canine is blade-like and procumbent like I_3 but the mesial taper is less marked and the protoconid projects occlusally. Midway along the distal crest of the protoconid is a concave, buccally bevelled facet caused by contact with the upper canine. The mesial interstitial facet is in the same position as on I_3.

P_1 is less blade-like, has a rounded distolingual shelf, a small talonid cusp and a shorter mesial overhang than in the canine. The mesial interstitial facet is more horizontal and is further under the mesial overhang. M35673 has a more delicate cuspate aspect than the other specimens and might be a deciduous tooth.

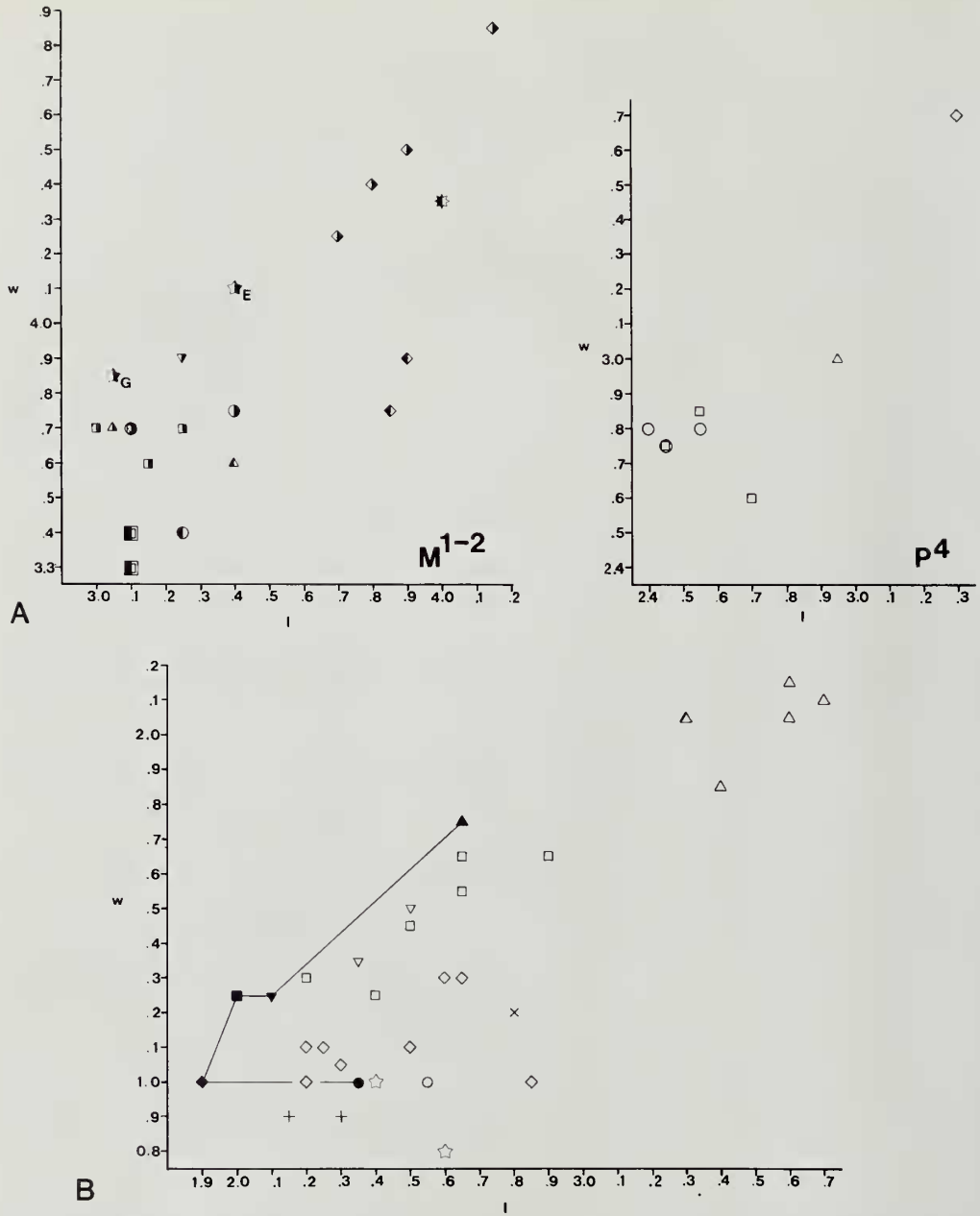
P_2 is less procumbent than P_1, has very weak development of metaconid and protostylid (often situated low down on the distal slope of the protoconid) and the talonid consists of a transverse ridge forming the distal crown margin and rising buccally to form a small ?hypoconid.

P_3 is like P_2 but relatively shorter, more upright, less procumbent, and with a distinct mesially projecting paraconid. It thus contrasts with *A. eocaenicus* in which P_3 is almost identical to P_2. An alternative is that some P_3s have been misidentified as P_2s. From alveolar evidence, this and all the more mesial teeth were single-rooted, those more distal double-rooted.

P_4 is much the same as in *G. grisollensis* but the preprotocristid appears to have a more buccal sweep and the paraconid may be bicuspid.

Two trigonid fragments are identified as DP_4 on the basis of low crown height, thin enamel and mesially projected paraconid region. Protoconid and metaconid are subequal in height. M35684 is unworn and shows a papillate paraconid.

Of the lower preultimate molars, one can be confidently assigned to M_2, as the tip of its broken root was found *in situ* in an otherwise edentulous mandibular fragment (M35407). The tooth has been restored to its original position in the jaw. There is less difference between its mesial and distal width measurements than some isolated teeth which also have a longer trigonid. The latter are here identified as M_1. Overall morphology is almost identical to that of *G. grisollensis* M_1s and M_2s.



Text-figure 14 A, scatter diagrams of length (l) against width (w) in M^{1-2} and P^4 of species of *Gesneropithex*. △ = *G. latidens* (Teilhard); □ = *G. grisollensis* (Louis & Sudre) from Grisolles; ○ = *G.* aff. *grisollensis* from the Hordle Cliff Mammal Bed; ▽ = *G.* aff. *grisollensis* from Hordle Cliff (Rodent Bed?); ◇ = *G. figularis* sp. nov. from Creechbarrow; ☆ = *G. peyeri* Hürzeler from Gösgen Pumpstation (G) and Eclépens B (E); ✲ = *G.* sp. indet. from Robiac. Symbols filled in on left are M^1s, those filled in on right are M^2s. B, scatter diagram of length against width in $I_{1?}$–P_4 of *Gesneropithex figularis* from Creechbarrow (crosses and outline symbols) and C_1–P_4 of *Amphilemur eocaenicus* Heller (syntype GH.7416) from Geiseltal (solid symbols linked by line). × = $I_{1?}$; + = I_2; ☆ = I_3; ○ = C_1; ◇ = P_1; □ = P_2; ▽ = P_3; △ = P_4. Measurements in millimetres.

M_3 shows considerable variation in size and hypoconulid development. The hypoconulid may be nearly as large as the entoconid, situated slightly lingual to the midline and distinctly separated from either entoconid or hypoconid (e.g. M37130) or it may be smaller, lingual in position and completely fused to the entoconid (e.g. M35410). M35688 is intermediate in morphology. Louis & Sudre (1975) described M_3 of *G. grisollensis* from three teeth whose morphology is like M37130.

Relationships. There appear to have been at least four lineages of *Gesneropithex* in total, spanning Auversian to mid-Ludian (viz. *G. peyeri*, *G. grisollensis–latidens*, *G. figularis* and the *G.* sp. from Robiac). They were probably derived from a species of *Amphilemur* of the early to middle Lutetian, but curiously no member of the Amphilemuridae is known from the rich late Lutetian to Auversian Egerkingen fissure deposits. Louis (1976: 49), however, recorded some teeth from the Auversian locality of Arcis-le-Ponsart, which he considered were close to *G. grisollensis*.

Additional records of *G. peyeri*, as used in comparisons in this paper (e.g. Text-fig. 14A) are based on an unworn M^2 (NMB Mt1227) and a DP^4 (NMB Mt1465) from Eclépens B. It is also probable that the M^1 and DP^4 figured by Sudre (1969*a*, 1978*b*) as dichobunid artiodactyls belong to the same species as his *G.* sp. from Robiac (Sudre 1969*b*). The hypocone being larger than the metaconule on both would be unusual for *Mouillacitherium*, as he himself noted (1978*b*), and also for artiodactyls generally. The outline and cusp pattern is typical of *Gesneropithex* and probably represents a new species. An M_2 (CGH RC29) from Robiac is virtually unworn and shows some special features.

G. figularis appears closely related to *G. grisollensis*, which in turn is almost indistinguishable from *G. latidens* in many features. Comparisons are also hampered because the holotype of *G. latidens* is unique and from an unknown stratigraphical level. There is some variation in development of the 'erinaceid' crest in *G. grisollensis* despite Louis & Sudre's (1975) statement. On *G. latidens* there is overall less cresting of the cusps, longer mesial upper molar cingula and more continuous ectocingulum, but it is not clear whether this is merely individual variation. Specimens of *Gesneropithex* from the Mammal Bed and ?Rodent Bed, Hordle Cliff, are difficult to classify, some looking like *G. grisollensis*, others more like *G. latidens*. None have the P^4 distal cingulum bypassing the incipient hypocone and passing lingually, or such a weak distal hypocone crest as in *G. latidens*; in P^4 size the Mammal Bed specimens are more like *G. grisollensis*, but the P_4 metaconid appears to be smaller.

Species of *Gesneropithex* have a patchy stratigraphical and geographical distribution so it is not surprising to find a new species at Creechbarrow. It seems likely that *G. figularis* became extinct before the Ludian, being replaced in southern England by the smaller *G.* aff. *grisollensis*.

Family **NYCTITHERIIDAE** Simpson 1928

The modern concept of this family was first proposed by Robinson (1968). European members were treated in detail by Sigé (1976) who divided the family into two subfamilies: Nyctitheriinae Simpson 1928 and Amphidozotheriinae Sigé 1976. Earlier history of the family was briefly given by Cray (1973: 36) and need not concern us here.

Subfamily **NYCTITHERIINAE** Simpson 1928

Type genus. *Nyctitherium* Marsh 1872.

Included genera. *Leptacodon* Matthew & Granger 1921; *Saturninia* Stehlin 1940; *Scraeva* Cray 1973; and *Pontifactor* West 1974.

Range. Middle Palaeocene to late Eocene, North America; early Eocene to early Oligocene, Europe.

Diagnosis. See Robinson (1968).

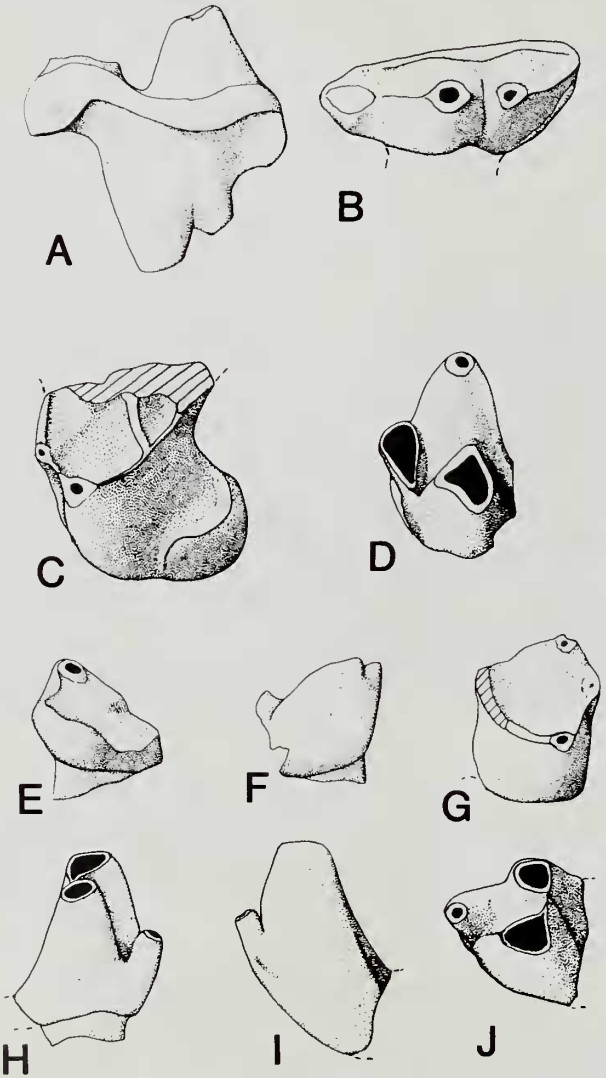
Genus *SCRAEVA* Cray 1973
[= *Arvaldus* Cray 1973]

TYPE SPECIES. *Scraeva hatherwoodensis* Cray 1973. *Microchoerus* Bed, upper Middle or lower Upper Headon Beds; Headon Hill, Isle of Wight.

INCLUDED SPECIES. *S. woodi* Cray 1973.

RANGE. Bartonian (Creechbarrow Limestone) to Ludian (Bembridge Limestone), southern England.

DIAGNOSIS. See Cray (1973: 37) and Sigé (1976: 11, 78).



Text-figure 15 *Scraeva* sp. indet., from Creechbarrow. All × 20. A–B, right P^4 fragment (reversed) (M35647). A is buccal and B occlusal view. C, occlusal view of left $M^{1/2}$ (M35648). D, occluso-buccal view of left lower molar trigonid (M35649). E–G, right $M_{1/2}$ talonid (reversed) (M35424). E is lingual view, F buccal and G occlusal view. H–J, right P_4 trigonid (reversed) (M35650). H is lingual view, I buccal and J occlusal view.

Scraeva sp. indet.
(Text-fig. 15)

v. *1977b* Nyctitheriidae indet.; Hooker: 141.
v *1980* *Scraeva* sp.; Hooker & Insole: 37.

MATERIAL. Right P^4 buccal fragment (M35647); two left $M^{1/2}$ fragments (M35422, M35648); right $M^{1/2}$ fragment (M37143); right P_4 trigonid (M35650); left $M_{1/2}$ talonid (M35423); right $M_{1/2}$ talonid (M35424); left lower molar trigonid (M35649).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. The material representing this taxon is poor, but both $M_{1/2}$ talonid fragments show the presence of a mesoconid, the only character by which this genus can be distinguished from *Saturninia* (see Text-fig. 15E). The size of the specimens appears intermediate between that of *S. hatherwoodensis* and *S. woodi*.

No upper teeth of *Scraeva* have been published, although two upper molars were figured in a thesis by Insole (1972: pl. 6, figs 1–2). The right P^4 fragment from Creechbarrow lacks the protocone. The connate paracone and metacone are tall cusps, the latter shorter and narrower than the former. The parastyle is prominent and the tooth was very waisted between the paracone/metacone region and the (now missing) protocone region. These last two characters are present in Sigé's (1976: 41, fig. 46; 42, fig. 48) figures of P^4s of *Saturninia hartenbergeri* Sigé 1976. In *Saturninia* the P^4s especially are intraspecifically variable for some features (see Sigé 1976: 22, fig. 12), but it is noteworthy that the paracone and metacone are lower and further apart in *Scraeva woodi* and *Saturninia gracilis* than in M35647.

The best preserved of the three $M^{1/2}$s (M35648) is lacking the buccal region along with the parastyle, paracone, metacone and metastyle. The postparaconule crista is weak but the premetaconule crista is strong as in *S. woodi*. The hypocone is prominent and the postflexus is deep as in *S. woodi*. The precingulum is weak like *S. woodi*, not as strong as is usual in *S. hartenbergeri*. The development of the premetaconule crista is like not only *S. woodi* but also *Saturninia grisollensis* Sigé 1976 and *S. hartenbergeri*.

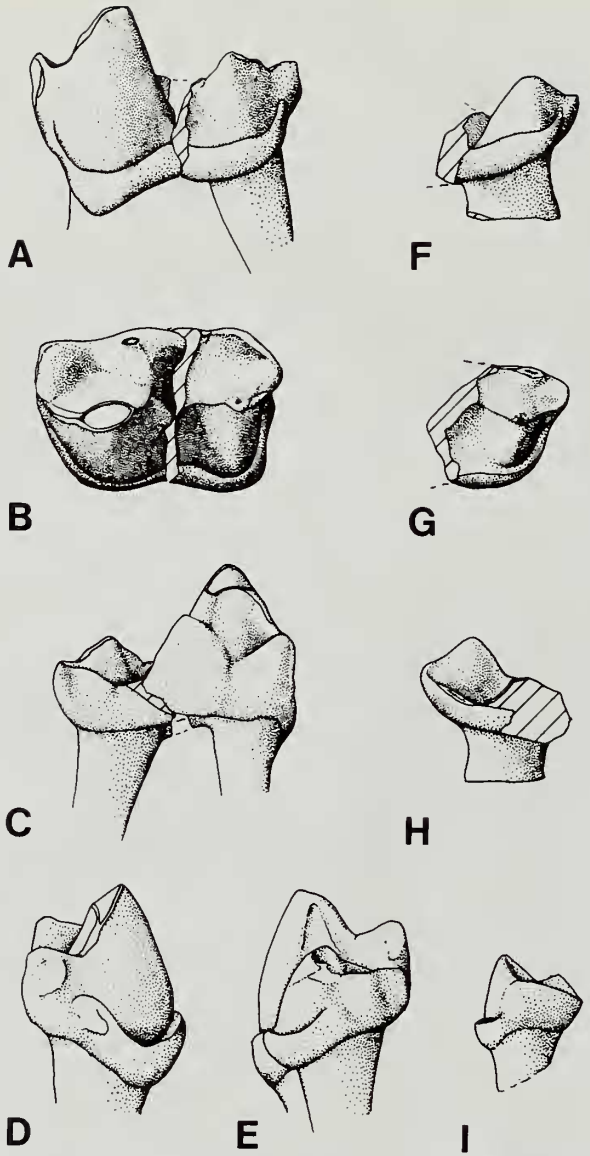
The P_4 trigonid, although slightly worn, appears overall higher than in *S. hatherwoodensis* or *S. woodi*. This would fit with the relatively high paracone and metacone of P^4. The metaconid appears relatively higher than in *S. hatherwoodensis* but this feature seems variable in *S. woodi*.

COMMENTS ON THE STATUS OF *Scraeva*. It is accepted that *Scraeva* and *Saturninia* are very closely related (see Sigé 1976: 78–79), but on the basis of the meagre Creechbarrow material their dichotomy must have been before the Bartonian. Oddly, however, Sigé's (1976: 57, fig. 73) figure of $M_{1/2}$ of *Saturninia grandis* Sigé 1976 shows a mesoconid. Sigé did not mention the character in his description. As *S. grandis* is the largest species of *Saturninia*, approximately equal in size to *Scraeva woodi*, it is worth considering the possibility that the presence of a molar mesoconid is purely a feature of large size, not of generic relationships. This argument is weakened by the fact that another large species of *Saturninia*, *S. beata*, apparently has no mesoconid. It is also possible of course that *Saturninia grandis* should be considered a *Scraeva*. Conclusions of this kind cannot be made on the basis of the poor material from Creechbarrow but must await fuller study of material from the Fluvio-marine series in comparison with *Saturninia* species.

Order **CHIROPTERA** Blumenbach 1779
Suborder **MICROCHIROPTERA** Dobson 1875
Microchiroptera gen. et sp. indet. 1
(Text-fig. 16)

v. *1972* ?Omomyoidea indet.; Hooker: 180–181.
vp. *1980* Chiroptera indet.; Hooker & Insole: 38.

MATERIAL. Left lower molar trigonid fragment (M35710); left $M_{1/2}$ talonid fragment (M35712); right M_3 talonid fragment (M29090).



Text-figure 16 Microchiroptera gen. et sp. indet. 1. A–E, left lower molar trigonid fragment (M35710) and left $M_{1/2}$ talonid fragment (M35712), almost certainly same specimen, from Creechbarrow. Views: A, buccal; B, occlusal; C, lingual; D, mesial; E, distal. F–I, right M_3 talonid fragment (reversed) (M29090) from the Barton Clay (Bed F?), Barton. Views: F, buccal; G, occlusal; H, lingual; I, distal. All × 16·5.

HORIZONS AND LOCALITIES. M29090 is from the Barton Clay (probably around Bed F), Barton Cliff at Barton-on-Sea; the others are from the Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. M35710 and M35712 were found in the same excavation hole. Although they are of identical preservation, size and wear their actual physical fit is poor. Nonetheless this is probably due to abrasion during weathering of the limestone and they almost certainly belong

to the same specimen, a left $M_{1/2}$. Its length is estimated 2·00 mm, the trigonid width is 1·22 mm and talonid width 1·25 mm.

It is a robust, fairly low-crowned tooth. It is somewhat worn on the lingual sides of the protoconid and hypoconid tips and the paracristid. There are extensive buccal phase facets on the mesiobuccal walls of the protoconid, precingulid and hypoconid and smaller ones on the distobuccal edges of the protocristid, postmetacristid, postcristid and hypoconulid. The tip of the hypoconid is chipped on the buccal side. There is a continuous buccal cingulum terminating with the precingulid and postcingulid. This parallels the basal crown margin which undulates round the trigonid, reaching a low point at the mesiobuccal corner. There is essentially no ectoflexid. There are abraded patches on the mesial sides of the paraconid and the lingual end of the precingulid, but it is not certain whether or not they represent interstitial facets.

The trigonid is long but the paracristid curves lingually to join the paraconid. The metaconid is a prominent cusp, very slightly higher than the paraconid but much lower than the protoconid. It is strongly salient mesial of the deeply notched protocristid. The protoconid has a prominent lingual rib. The talonid is much lower than the trigonid, and narrower at the cusp tips although the same width basally. The hypoconulid is only slightly nearer the entoconid than the hypoconid, thus not being truly nyctalodont (see Menu & Sigé 1971). An important feature is the very low crestiform entoconid, which is little more than an occlusally convex bulge of the entocristid and lower than the hypoconulid. The cristid obliqua is essentially longitudinal, slightly concave buccally and joins the protoconid just buccal of the trigonid notch.

M29090 is smaller than M35712 (0·93 mm wide) and has no distal interstitial facet. It is slightly narrower and the hypoconulid protrudes further distally. The entoconid is worn but was of similar morphology to M35712, although probably even lower. In other respects the two talonids are almost identical.

The curious character of the entoconid in both suggests that they may belong to the same taxon.

Discussion. The hipposiderid *Palaeophyllophora* Revilliod 1917*b* is similar in having a relatively low semi-nyctalodont talonid with often weak entoconid (see Sigé 1978: pl. 1, fig. 2). However, the entocristid is nevertheless high, the whole tooth is higher-crowned, the talonid is shorter relative to the trigonid, the paracristid is obliquely straight and the cusps are less prominent.

The archaeonycterine palaeochiropterygid *Archaeonycteris* Revilliod 1917*a* has a lower molar trigonid rather similar to the Creechbarrow specimen (see Russell & Sigé 1970: pl. 6, figs 1c, 3). It also has a similarly-placed hypoconulid and can have a fairly weak entoconid (see Russell *et al.* 1973: text-fig. 6i).

Other European Palaeogene bats show little in common with this taxon from Creechbarrow and Barton. The low tubercular nature of the teeth and the near median hypoconulid are primitive characters and suggest affinities with the superfamily Palaeochiropterygoidea Revilliod 1917*a*. The special entoconid character perhaps suggests closer affinities with *Archaeonycteris* than with any other genus, but certain other specializations are probably only convergent with *Palaeophyllophora*. Should it become better known, it may be found to be a new genus.

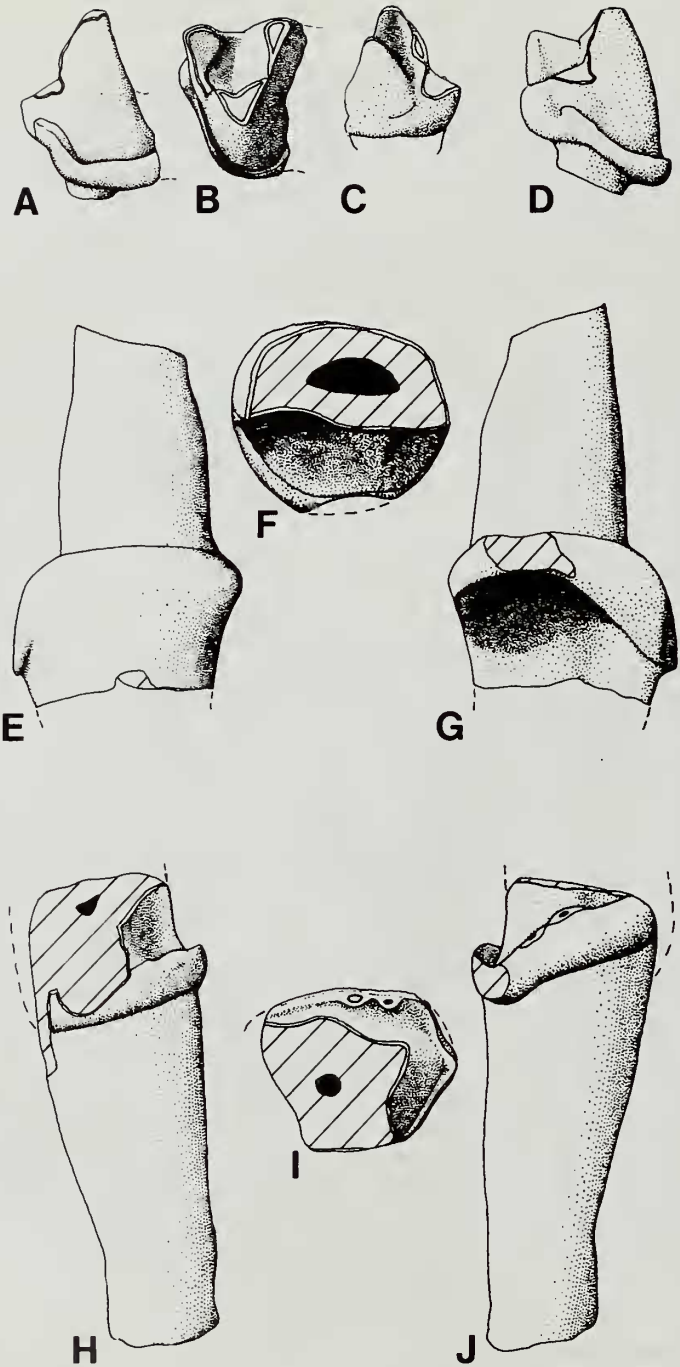
Microchiroptera gen. et sp. indet. 2
(Text-fig. 17A–D)

vp. *1980* Chiroptera indet.; Hooker & Insole: 38.

Material. Left lower molar trigonid (M35711).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. The fragment is 1·17 mm wide. The trigonid is buccally acute with a straight, slightly oblique paracristid. The buccal cingulum is complete to the precingulid. The metaconid



Text-figure 17 Microchiroptera from Creechbarrow. A–D, left lower molar trigonid fragment (M35711) of Gen. et sp. indet. 2. Views: A, buccal; B, occlusal; C, lingual; D, mesial. E–G, left upper canine (M36790) of Gen. et sp. indet. 3. Views: E, buccal; F, occlusal; G, lingual. H–J, left lower canine (M36421) of Gen. et sp. indet. 4. Views: H, buccal; I, occlusal; J, lingual. All × 16·5.

is slightly salient mesially. The protoconid is concave lingually. The paraconid is heavily worn and would probably have been slightly lower than the metaconid. The edges of the paracristid and protocristid and the tips of the protoconid and metaconid are slightly worn. The tooth as a whole is slightly corroded.

Discussion. The fragment is more gracile, more crestiform and has higher cusps than M35710, which also differs in many of the characters described. It must therefore represent a different taxon from Microchiroptera gen. et sp. indet. 1. Unfortunately the talonid is missing and the morphology of the trigonid could be encountered in a very wide variety of microchiropteran taxa.

Microchiroptera gen. et sp. indet. 3
(Text-fig. 17E–G)

Material. Left upper canine (M36790).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. Much of the main cusp is broken away and parts of the lingual cingulum are abraded. In occlusal view the tooth is subovoid in outline. The strong shelf-like lingual cingulum continues round the mesial edge where it migrates further up the crown. Distobuccally there is a slight ridge-like basal swelling not developed into a true cingulum. The lingual side of the main cusp is concave, the buccal side convex. Length is 1·77 mm, width 1·53 mm.

Discussion. What is preserved of this tooth is very like the hipposiderid *Pseudorhinolophus* Schlosser 1887, especially in the lingual concavity. A slight difference is that the lingual cingulum is slightly shallower at its distal end. Size is similar to that of *P. weithoferi* Revilliod 1917*b*. If the similarities indicate true affinities with this genus, M36790 cannot belong to Microchiroptera gen. et sp. indet. 1. Although Microchiroptera gen. et sp. indet. 2, amongst many other taxa, could fit in the genus *Pseudorhinolophus*, it is a little small for this upper canine, M36790, to be associated with it.

Microchiroptera gen. et sp. indet. 4
(Text-fig. 17H–J)

Material. Left lower canine (M36421).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. Most of the main cusp is broken away leaving only the distal and lingual areas of the base of the crown together with the root. There is a strong cingulum continuous round the region preserved. The latter is slightly cuspate distally and there are two worn papillae lingually. The main cusp has a prominent lingual rib and a distolingual crest.

Discussion. The mesiolingual angle is more acute than it is in *Pseudorhinolophus* and the lingual cingulum is stronger, so it is unlikely that this tooth belongs to the same taxon as Microchiroptera gen. et sp. indet. 3, but on grounds of size it could belong to either of the other two. It is too incomplete for further comment.

Order **PRIMATES** Linnaeus 1758

Suborder **PROSIMII** Illiger 1811

Infraorder **TARSIIFORMES** Gregory 1915

Family **OMOMYIDAE** Trouessart 1879 (*sensu* Szalay 1976)

Subfamily **MICROCHOERINAE** Lydekker 1887 (*sensu* Simons 1961)
(including Necrolemurinae Simpson 1940 and Pseudolorisinae Simpson 1940)

Type genus. *Microchoerus* Wood 1844.

Included genera. *Pseudoloris* Stehlin 1916, *Nannopithex* Stehlin 1916, *Necrolemur* Filhol 1873 and ?*Pivetonia* Crusafont-Pairo 1967.

RANGE. Late Ypresian to late Ludian, Europe.

INTRODUCTION. I follow Szalay (1976; see especially pp. 168–170 for historical review) in allocating this subfamily to the Omomyidae, rather than Russell *et al.* (1967), who placed it in the Tarsiidae. This is done on grounds of greater morphological similarity. Classically separated from the North American Omomyidae essentially on geographical grounds, the Microchoerinae appear not to have been diagnosed since they have acquired the present generic content, nor since being placed in the present family. It is almost certainly a natural group, as Simons (1961) thought. Szalay (1976: 413) considered that the only features of the Microchoerinae which might separate them from the other omomyids was tibiofibular fusion and extreme inflation of the mastoid, and that the enlarged first lower incisor was a primitive

Table 6 Coefficients of variation for length and width of teeth of Recent *Tarsius*.

		T. bancanus borneanus		*T.b.b. + T. syrichta*		*T.b.b. + T.b. natunensis*		*T.b.b. + T.b.n. + T. syrichta*	
Tooth		N	v	N	v	N	v	N	v
I^1	l	8	4·45	10	8·41	9	4·63	11	8·04
	w	8	9·54	10	10·78	9	9·59	11	10·50
I^2	l	7	4·35	8	4·65	8	5·63	9	5·57
	w	7	4·47	8	10·02	8	4·17	9	9·37
C^1	l	8	4·33	10	5·37	9	5·49	11	5·87
	w	8	4·94	10	9·97	9	4·83	11	9·46
P^2	l	7	4·73	10	7·44	8	7·14	11	8·06
	w	7	3·00	10	11·02	8	3·97	11	10·49
P^3	l	8	7·94	10	7·69	9	7·81	11	7·55
	w	8	3·46	10	3·15	9	3·24	11	3·00
P^4	l	8	5·63	10	5·19	9	6·17	11	5·65
	w	8	5·43	10	5·29	9	5·36	11	5·28
M^1	l	8	3·68	10	3·50	9	3·69	11	3·54
	w	8	2·39	10	3·53	9	2·58	11	3·61
M^2	l	7	2·94	9	2·95	8	3·06	10	3·07
	w	7	2·29	9	2·86	8	2·12	10	2·70
M^3	l	8	4·50	10	4·08	9	4·21	11	3·87
	w	8	5·87	10	5·32	9	5·59	11	5·12
I_1	l	7	3·92	8	4·11	8	4·11	9	4·17
	w	7	7·97	8	7·67	8	8·62	9	8·44
C_1	l	7	5·30	8	5·67	8	6·22	9	6·26
	w	7	7·16	8	7·19	8	6·87	9	6·87
P_2	l	7	6·69	9	6·52	8	7·64	10	7·15
	w	7	3·61	9	9·37	8	5·63	10	9·33
P_3	l	7	5·47	8	5·97	8	5·49	9	5·83
	w	7	5·63	8	6·14	8	5·21	9	5·75
P_4	l	8	8·08	9	7·80	9	9·11	10	8·70
	w	8	6·63	9	6·20	9	7·02	10	6·63
M_1	l	8	5·60	10	4·99	9	5·30	11	4·82
	w	8	3·14	10	3·75	9	4·97	11	4·93
M_2	l	7	6·09	9	5·43	8	5·78	10	5·30
	w	7	3·82	9	3·51	8	5·34	10	4·80
M_3	l	8	3·74	10	3·60	9	4·27	11	4·11
	w	8	4·26	9	4·05	9	5·40	10	5·10

feature of the subfamily. Szalay & Delson (1979: 258) considered the conformation of the enlarged upper and lower first incisors as the primary diagnostic feature. Slight separation of the first pair of upper incisors was considered to differentiate them from the Tarsiidae and other omomyids where the anterior dentition was known. Most of these features are omitted from the diagnosis below as they are known for so few of the genera in the whole family that their value cannot be reasonably assessed.

Dental formula. This was interpreted by Simons (1961) as $\frac{2\ 1\ 3\ 3}{0/1\ 1\ 4\ 3}$. Small perforations in the lower jaw anterior to the enlarged lower tooth were thought by him to be the alveoli of a very small incisor. These were reinterpreted by Gingerich (1975*a*, 1976*b*) and Szalay (1975, 1976) as anterior mental foramina. Gingerich (1976*b*: 91) reinterpreted the lower formula as 1 1 3 3 by direct comparison with *Tarsius*. Szalay (1976) in contrast interpreted it as 2 1 2 3 by direct comparison with *Omomys* or *Tetonius* (presumably with respect to their mode of tooth reduction rather than their actual dental formula). If one considers details of occlusion in *Microchoerus* (see Simons 1961: text-fig. 2) it is more reasonable that P^2 should occlude with an equal-sized P_2 rather than with the lower canine as it would have to according to Szalay's interpretation. The small tooth immediately distal to the enlarged lower incisor could then be either the lower canine or I_2. As the larger of the two alternatives in the upper jaw is the canine, it is almost certain that this is the one which would be retained. Thus Gingerich's interpretation of the dental formula is followed here. Consequently it seems that reduction and loss for face shortening has involved teeth different in the Microchoerinae from the Omomyinae or Anaptomorphinae.

Emended diagnosis. Dental formula: $\frac{2\ 1\ 3\ 3}{1\ 1\ 3\ 3}$. $I\frac{1}{1}$ enlarged; upper canine and P^2 subequal, not greatly reduced, approximately same length as P^3; P_{2-3} subequal, slightly smaller than P_4; I^2 and lower canine greatly reduced.

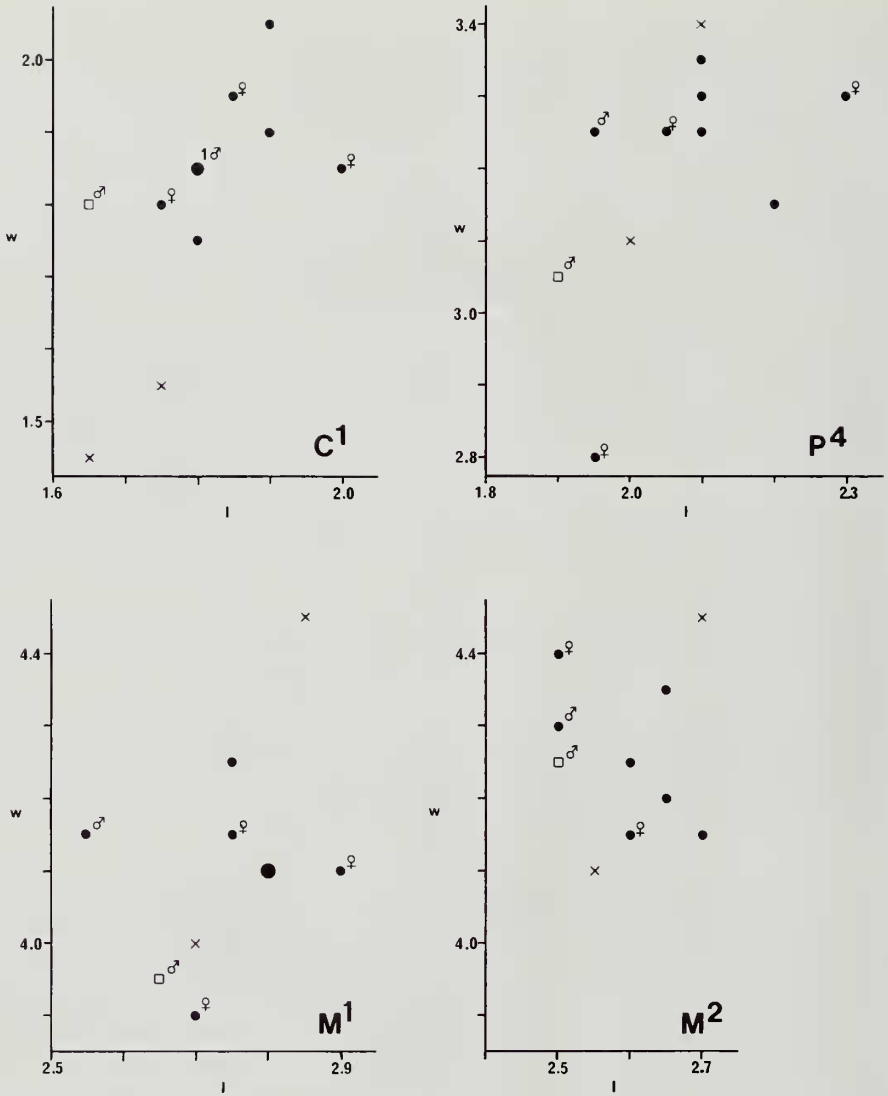
Origins. It is unlikely that the subfamily is derived from *Teilhardina* as Hürzeler (1948*b*) thought, because *Nannopithex* occurs by the late Ypresian (see Hooker & Insole 1980: 38) with already too great modification of the anterior dentition (i.e. enlargement of $I\frac{1}{1}$). As yet fragmentary omomyid remains from the English early Eocene (Hooker 1980, Hooker & Insole 1980) might provide alternative candidates.

Recent comparative material. Because of small sample sizes of this subfamily in the Creechbarrow assemblages, and because ranges of variation in some published measurements of *Microchoerus* species are large, I sought an independent control. In searching the literature for tooth measurements of the Recent tarsiid *Tarsius*, I found that Swindler (1976: 68, 210–211, tabs 43–46) gave statistics for length and width of $C\frac{1}{1}$–$M\frac{3}{3}$. Unfortunately Swindler pooled the different species to increase the number of measurements. I have calculated the coefficients of variation of these measurements and the majority are indeed higher than normally found in a single species (see Gingerich 1974). The numbers of specimens available to Swindler were: *T. spectrum* (1 male, 5 females), *T. bancanus* (1 male, 1 female), *T. syrichta* (7 males, 9 females).

I therefore measured the length and width dimensions of all the teeth of Recent *Tarsius bancanus* and *T. syrichta* available in the BM(NH) Zoology Department (a maximum of 12 specimens). The coefficients of variation are given in Table 6, and plots of certain teeth in scatter diagrams in Text-fig. 18. Gingerich (1974: 896) demonstrated that low coefficients of variation (v) were characteristic for cheek teeth of a range of mammalian taxa, mainly primate (from various sources). This did not include *Tarsius*.

Tarsius, as far as the relatively small sample of mainly one species can show, has generally low coefficients of variation for all the teeth. Intraspecific variation is high only in I^1 width, P^3 length, I_1 width, lower canine width and P_4 length. M_1 and M_2 length is more variable than in the corresponding upper teeth and may result partly in variation in size and position of the paraconid and also in its wear. P_4 length variation may be artificially high because it is difficult to measure, being oblique in side view.

The largest sample was of *T. bancanus borneanus* from Borneo. Numbers of other species or subspecies were too low to be compared for v, other than by adding to the data for *T. bancanus*



Text-figure 18 Scatter diagrams of length (l) against width (w) in upper canine, P^4, M^1 and M^2 of species of Recent *Tarsius*; × = *T. syrichta* (Linné) from the Philippines; ● = *T. bancanus borneanus* Elliott from Borneo; □ = *T. bancanus natunensis* Chasen (type) from the S. Natuna Islands. Individuals of known sex are indicated. An enlarged solid circle indicates two identical measurements. Measurements in millimetres.

borneanus to see whether this was then increased or decreased. Either or both happened with the more anterior teeth, but the molars were much more constant (see Table 6). For application of these data to the Creechbarrow microchoerines, see under the relevant species.

Niemitz (1977) made a biometrical study of Recent *Tarsius* and reduced the recognizable species to three, and subspecies to two of *T. spectrum*, possibly two of *T. bancanus* and one of *T. syrichta*. He did not measure the teeth but, comprehensively done, this would seem a worthwhile project. Although the populations of *Tarsius* on the various Far Eastern islands

cannot have been separated for long geologically, it is evident that isolation has produced slightly different dimensions for some of the teeth, mainly the unicuspid anterior ones.

NOTE ON MEASUREMENTS. Because of the problem in deciding on the mesiodistal and buccolingual parameters in $I\frac{1}{1}$, the length and width dimensions given for these teeth alone (including Recent *Tarsius*) are anteroposterior and mediolateral respectively.

Genus *NANNOPITHEX* Stehlin 1916

TYPE SPECIES. *Nannopithex pollicaris* Stehlin 1916. Late Lutetian fissure fillings; Egerkingen, Grey Marl Facies (= Huppersand), Switzerland [= *Necrolemur filholi* Chantre & Gaillard 1897, Auversian fissure filling; Lissieu, France (*fide* Simons 1961: 66–67)].

INCLUDED SPECIES. *N. raabi* (Heller 1930) Simons 1961, *N. quaylei* sp. nov. and *N.* sp. 1. Szalay (1971*a*: 2) synonymized *Pivetonia* Crusafont-Pairo 1967 with *Pseudoloris*. From Crusafont-Pairo's figures, the M_{1-2} paraconids and long trigonids are more suggestive of *Nannopithex*, although size is close to *Pseudoloris parvulus*. Whatever the correct genus, *Pivetonia isabenae* Crusafont-Pairo 1967 is a valid species.

RANGE. Late Ypresian to Bartonian (Marinesian), England, France, East Germany and Switzerland.

EMENDED DIAGNOSIS. Tooth enamel wrinkling may be present; mesiolingual crest from paracone on I^2–P^4 absent; P^{3-4} paracone–protocone crest present: P^4 metastylar wing short; upper molar *Nannopithex* fold present; M^{1-2} outline subtriangular to subquadrate, broader than long; M^{1-2} hypocone usually much smaller than protocone; M^{1-2} paracone single and metaconule small and usually single; M^{1-2} mesostyle absent; I_2 narrow with distolingual cingulum strong; P_{2-3} relatively moderately elongated with high distal cingula; M_1 trigonid length $\geqslant$ talonid; M_{1-2} protocristid straight and complete; M_{1-2} entoconid lower than metaconid; M_{1-2} hypoconulid very small and single to absent; M_3 hypoconulid lobe moderately broad, short to long, unicuspid to bicuspid; paraconid present on M_{1-2}, usually fusing with metaconid on M_3; angular process may not be expanded; coronoid process may be high.

Nannopithex quaylei sp. nov.

(Pl. 4, figs 9–14; Pl. 5, figs 1, 5; Pl. 6, fig. 1; Text-figs 19–21)

v *1977b* ?*Pronycticebus* sp.; Hooker: 141.
v *1980* *Pseudoloris* sp. 1; Hooker & Insole: 39.

NAME. After Mr W. J. Quayle, for help with field work.

HOLOTYPE. Left M^2, M37145. Pl. 4, fig. 10.

PARATYPES (11). Left I^1 (M37154); right I^1 (M35434); left P^4 (M35759); two right P^4s, one almost complete (M35760), the other a buccal fragment (M37144); left M^3 lacking metaconal region (M35721); left I_1 (M35736); left P_3 (M35748); left $M_{1/2}$ talonid fragment (M35720); right $M_{1/2}$ talonid fragment (M35425); left M_3 talonid fragment (M37147).

DOUBTFUL MATERIAL. Four upper molar fragments (M35426, M35723, M36440, M37146); left M_3 trigonid fragment (M37152).

HORIZON AND LOCALITY.

DIAGNOSIS. Large *Nannopithex*, M^2 length 2·75 mm; tooth enamel surface smooth; P^4 parastyle distinct; M_3 with indistinct entoconid.

DIFFERENTIAL DIAGNOSIS. *N. raabi*, *N. filholi* and *N.* sp. 1 (p. 251) are smaller, have a distinct M_3 entoconid, the enamel wrinkled in varying degrees and an indistinct P^4 parastyle; *N. raabi* and *N. filholi* appear slightly higher-crowned; *N. filholi* sometimes has a larger M^{1-2} hypocone, broader bicuspid M_3 talonid and higher M_{1-2} entoconid.

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DESCRIPTION. Fragmentary representatives of several different important tooth types can be referred to this species. M_3^3s are not much larger than those attributed to *N.* sp. 1 (q.v.). The characters of the left M_3 talonid used in the diagnosis might be due partly to individual variation. More material is obviously needed (see Text-figs 19–21 for evidence of size separation from *N.* sp. 1).

Even though most of the teeth are slightly worn, this is not thought to have been the cause of lack of enamel wrinkling. The teeth of *N.* sp. 1 in the same states of wear still have visible wrinkling. The $M_{1/2}$ talonid fragments appear longer for their width than in the other *Nannopithex* species but trigonids are unknown.

Most of the other details of the teeth are typical of other *Nannopithex* species and evident from the figures (Pl. 4, figs 9–14, Pl. 5, figs 1, 5 and Pl. 6, fig. 1).

CONCLUSIONS. For the first time two contemporaneous species of *Nannopithex* at a single locality are demonstrated, as well as an upward extension of the range of the genus.

Nannopithex sp. 1
(Pl. 4, figs 1–8; Pl. 5, fig. 4; Text-figs 19–21)

v. *1977b Nannopithex filholi* (Chantre & Gaillard); Hooker: 141.
v. *1980 Nannopithex filholi* (Chantre & Gaillard); Hooker & Insole: 38.

MATERIAL. Left I^1 (M35728); right I^1 (M35740); left I^2 (M35741); right P^3 buccal half (M37151); right $P^{3/4}$ protoconal fragment (M37161); left M^2 broken buccally (M35724); right $M^{1/2}$ paraconal fragment (M35725); left M^3 protoconal fragment (M35722); left P_2 (M37149); two right M_1s (M35715–6); right $M_{1/2}$ talonid fragment (M35717); two left M_3s (M35427, M37153); right M_3 talonid fragment (M35727).

HORIZON AND LOCALITY.

DESCRIPTION. Much of the material from Creechbarrow is fragmentary, which makes accurate measurement difficult. The typically least variable teeth, the first and second molars, are especially incomplete whereas two M_3s are nearly complete.

Most of the specimens compare quite well with *N. filholi* (including *N. pollicaris*) but are larger. The enamel wrinkling is variable. The M^3 (M35722) is quite large and closer to *N. quaylei* in size than to any other described *Nannopithex* M^3s; it is tentatively distinguished on the enamel wrinkling. Two of the three M_3s (M35427, M37153) are similarly large but have wrinkled enamel in the talonid basin and a prominent entoconid. A tentative conclusion from this evidence is that *N.* sp. 1 has proportionately larger M_3^3s than *N. filholi*. An alternative explanation is that these teeth belong to *N. quaylei*. However, M35727 is rather smaller than the other two and more material is needed to be certain of this difference.

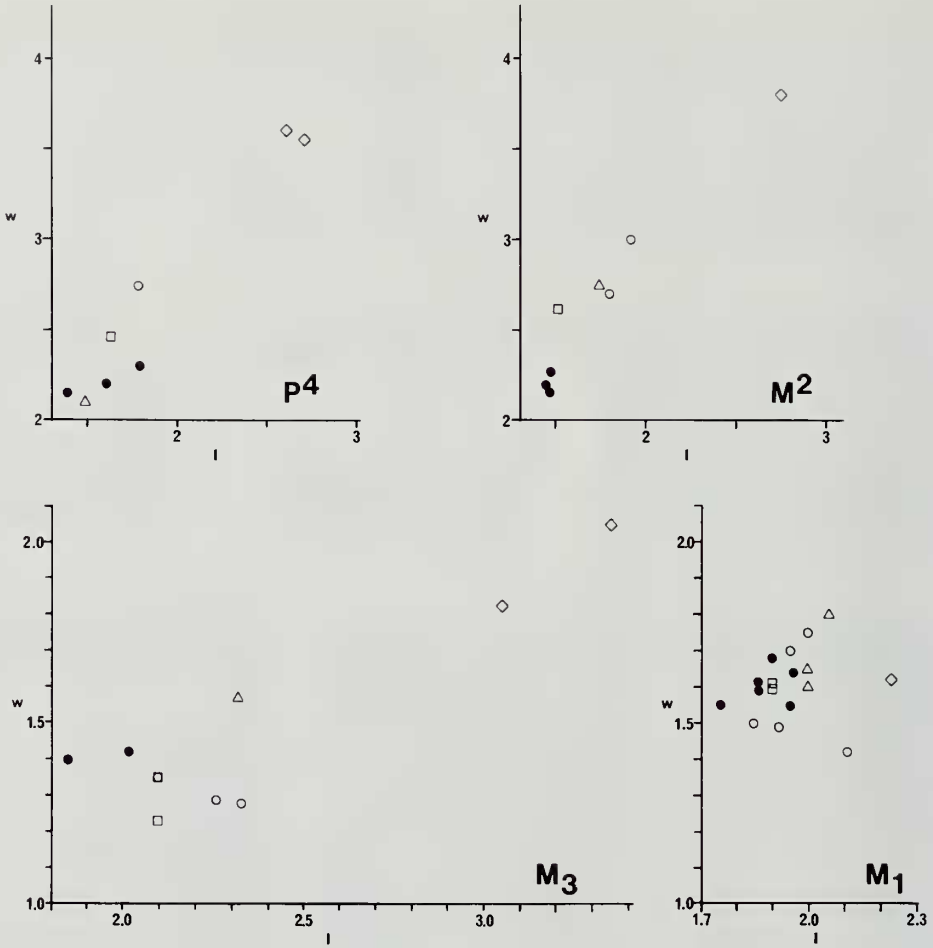
The M_1s (M35715–6) show, better than *N. quaylei*, the *Pseudoloris*-like elongation of the talonid (see Table 9). In this character and in slightly lower crown height they differ from *N. raabi* and *N. filholi*. A fairly close relationship to *Pseudoloris* may be indicated (see Text-fig. 24).

Text-figs 20–21 demonstrate the existence of size variation greater than expected for a single species of *Nannopithex* at Creechbarrow, but the fragmentary nature of some crucial tooth types renders *N.* sp. 1 unnameable in the present state of knowledge.

Plate 4 Scanning electron micrographs of occlusal views of teeth of *Nannopithex* from Creechbarrow, × 15.

Figs 1–8 *Nannopithex* sp. 1. Fig. 1, left I^2 (M35741). Fig. 2, buccal half of right P^3 (reversed) (M37151). Fig. 3, lingual half of right $P^{3/4}$ (reversed) (M37161). Fig. 4, lingual half of left M^2 (M35724). Fig. 5, lingual half of left M^3 (M35722). Fig. 6, left P_2 (M37149). Fig. 7, right M_1 (reversed) (M35715). Fig. 8, left M_3 (M35427). See above.

Figs 9–14 *Nannopithex quaylei* sp. nov. Fig. 9, right P^4 (reversed) (M35760). Fig. 10, **holotype** left M^2 (M37145). Fig. 11, left M^3 lacking metaconal region (M35721). Fig. 12, left P_3 (M35748). Fig. 13, right $M_{1/2}$ talonid fragment (reversed) (M35425). Fig. 14, left M_3 talonid fragment (M37147). See p. 249.



Text-figure 19 Scatter diagrams of length (l) against width (w) in P^4, M^2, M_3 and M_1 of species of *Nannopithex* from various European localities: ○ = Geiseltal (*N. raabi* (Heller)); □ = Bouxwiller (*N. raabi*); ● = Egerkingen γ and Grey Marl Facies (= Huppersand) (*N. filholi* (Chantre & Gaillard)); △ = Lissieu (*N. filholi*); ◇ = Creechbarrow. Data for Egerkingen and Lissieu mainly from Hürzeler (1948*b*). The Creechbarrow plots represent *N. quaylei* sp. nov. for the upper teeth and *N.* sp. 1 for the lowers. Measurements in millimetres.

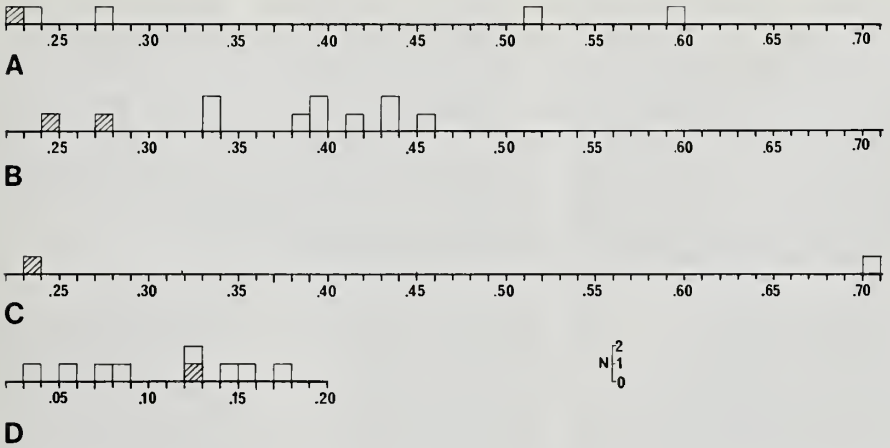
Genus ***PSEUDOLORIS*** Stehlin 1916

TYPE SPECIES. *Necrolemur parvulus* Filhol 1890*b*, from the Phosphorites du Quercy.

INCLUDED SPECIES. *P. reguanti* Crusafont-Pairo 1967 and *P. crusafonti* Louis & Sudre 1975.

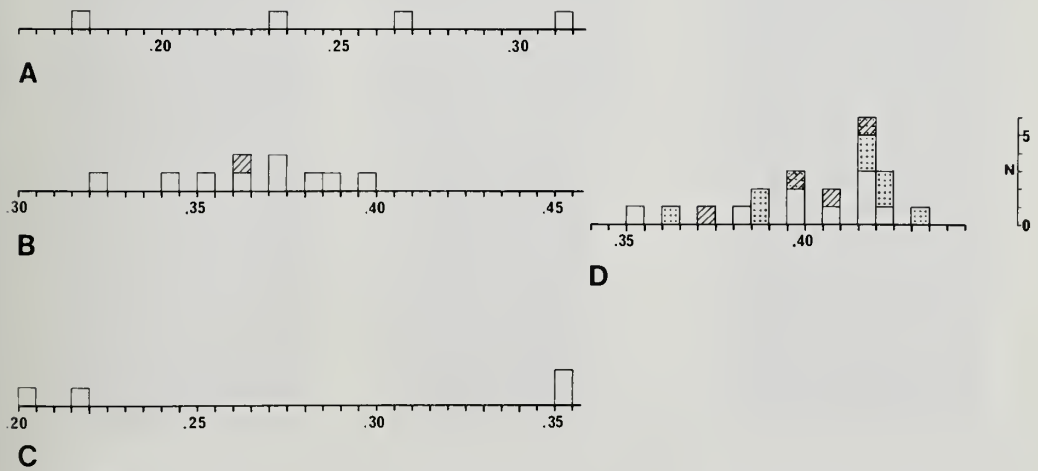
RANGE. Bartonian (Marinesian) to Ludian, England, France, Switzerland, West Germany and Spain.

EMENDED DIAGNOSIS. Tooth enamel wrinkling absent; mesiolingual crest from paracone on I^1–P^4 absent; P^{3-4} paracone–protocone crest absent; P^4 metastylar wing long; upper molar *Nannopithex* fold absent; M^{1-2} outline subtriangular, broader than long; M^{1-2} hypocone

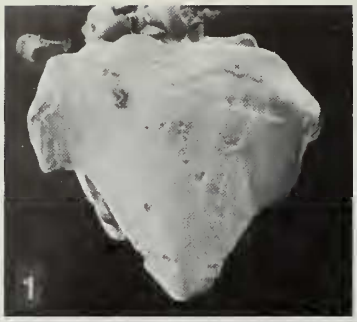


Text-figure 20 Histograms of log. length × width of: A, I^1 of *Nannopithex*; B, I^1 of Recent *Tarsius*; C, I_1 of *Nannopithex*; D, I_1 of Recent *Tarsius*. In A and C, hollow squares = *N. quaylei* sp. nov. and *N.* sp. 1 from Creechbarrow; hatched squares = *N. raabi* (Heller) from Geiseltal. In B and D, hollow squares = *T. bancanus* Horsfield; hatched squares = *T. syrichta* (Linné). Measurements in millimetres.

much smaller than protocone; M^{1-2} paraconule and metaconule small and single; M^{1-2} mesostyle absent; I_1 narrow with distolingual cingulum weak; P_{2-3} relatively very elongated with low distal cingula; M_1 trigonid length equal to talonid; M_{1-2} protocristid straight and complete; M_{1-2} entoconid same height as metaconid; M_{1-2} hypoconulid very small and single to absent; M_3 hypoconulid lobe narrow, short, unicuspid; lower molar paracristid without paraconid on M_{1-3} and not joined to metaconid by crest; angular process not expanded; coronoid process low.



Text-figure 21 Histograms of: A, log. talonid width of M_3 of *Nannopithex quaylei* sp. nov. and *N.* sp. 1 from Creechbarrow; B, log. maximum width of M_3 of Recent *Tarsius*, hollow = *T. bancanus* Horsfield, hatched = *T. syrichta* (Linné); C, log. talonid width of $M_{1/2}$ of *N. quaylei* and *N.* sp. 1 from Creechbarrow; D, log. talonid width of Recent *Tarsius*, hollow = *T. bancanus*, hatched = *T. syrichta*, dotted = M_2, undotted = M_1. Measurements in millimetres.



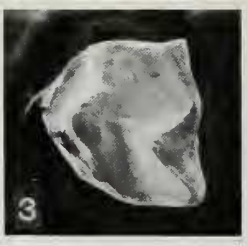


Plate 5 Scanning electron micrographs of teeth of *Nannopithex* and *Pseudoloris* from Creechbarrow, × 15.

Figs 1, 5 *Nannopithex quaylei* sp. nov. Fig. 1, buccal view of right P^4 (reversed) (M35760). Fig. 5a–c, right I^1 (reversed) (M35434); a, lateral (distobuccal), b, posterior (distolingual) and c, mesial views. See p. 249.

Figs 2–3 *Pseudoloris* cf. *crusafonti* Louis & Sudre. Fig. 2, occlusal view of right M^2 (reversed) (M37148). Fig. 3, occlusal view of right M_2 (reversed) (M35726), broken distally. See p. 256.

Fig. 4a–c *Nannopithex* sp. 1. Left I^1 (M35728); views as Fig. 5a–c. See p. 251.

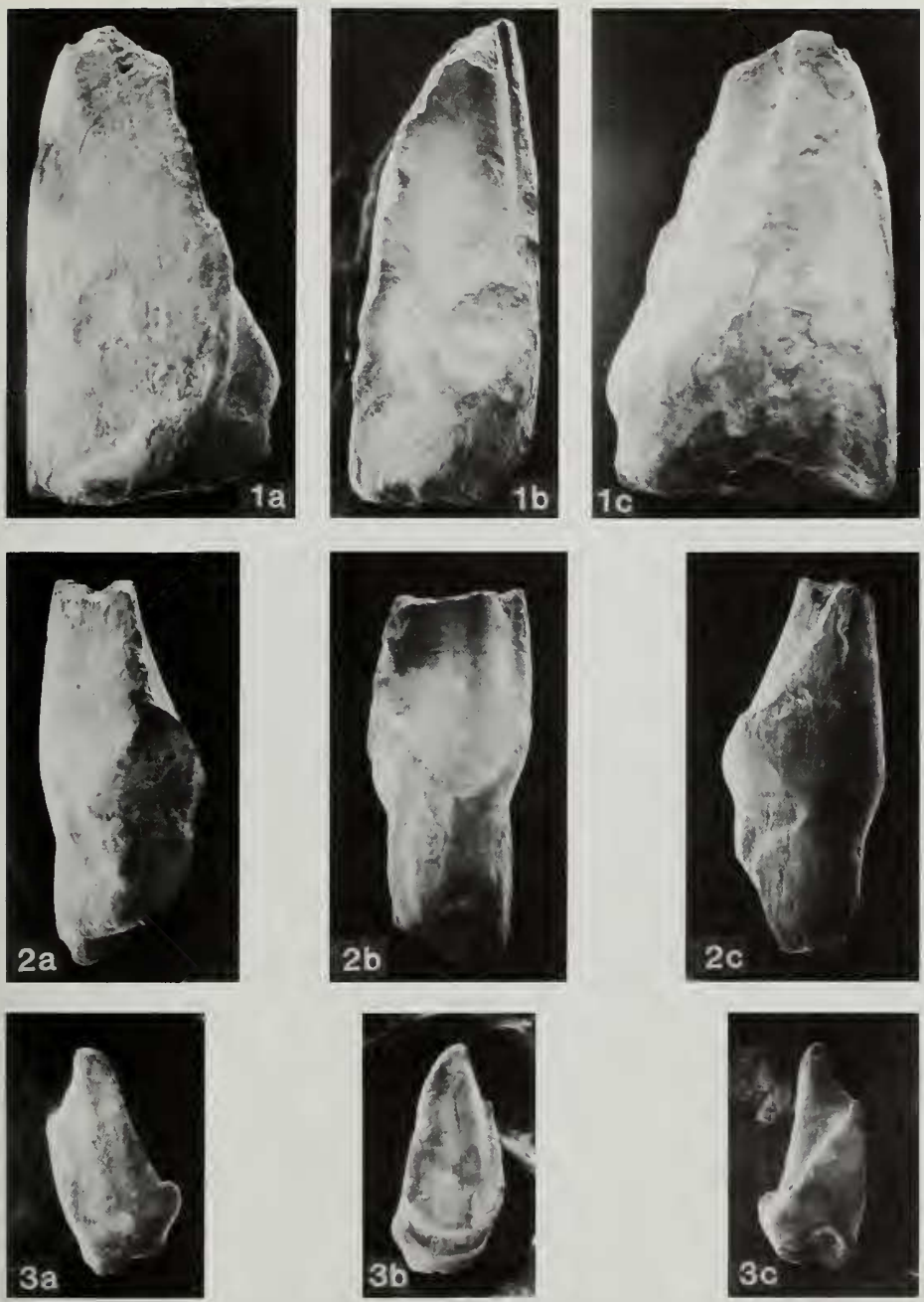


Plate 6 Scanning electron micrographs of lower incisors of *Nannopithex* and *Microchoerus* from Creechbarrow, × 15. Views as Pl. 5, fig. 5a–c.

Fig. 1a–c *Nannopithex quaylei* sp. nov. Left I_1 (M35736). See p. 249.

Figs 2–3 *Microchoerus wardi* sp. nov. Fig. 2a–c, left I_1 (M35747). Fig. 3a–c, left DI_1? (M35719). See p. 259.

Pseudoloris cf. *crusafonti* Louis & Sudre 1975
(Pl. 5, figs 2–3; Text-fig. 22)

v. *1977b Pseudoloris* cf. *crusafonti* Louis & Sudre; Hooker: 141.
v. *1980 Pseudoloris crusafonti* Louis & Sudre; Hooker & Insole: 39.

HOLOTYPE OF SPECIES. M^2 (UM GRI.443). Calcaire de St Ouen (Bartonian); Grisolles, Aisne, France.

DIAGNOSIS OF SPECIES. See Louis & Sudre (1975).

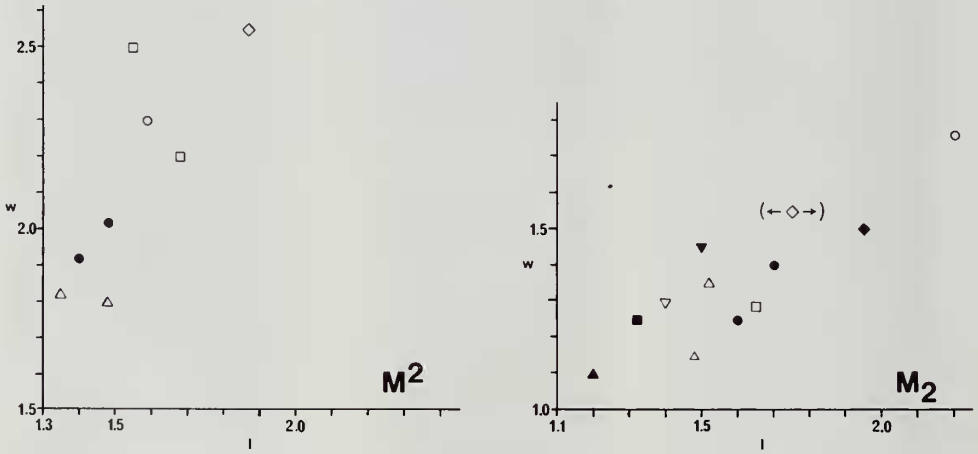
MATERIAL. Right M^2 (M37148) and right M_2 broken distally (M35726).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. *P. crusafonti* was considered by Louis & Sudre (1975) to be intermediate in size between *P. parvulus* and *P. reguanti*. Identification of the Creechbarrow material is complicated by Schmidt-Kittler's (1977*a*: 190–192, text-fig. 11) recent finds in the Ludian fissure filling of Weissenburg 8, southern Germany. On the basis of size, Schmidt-Kittler considered that two species were represented within the *P. crusafonti* assemblage from Grisolles, the lower molars overlapping with *P. parvulus*, the upper teeth being larger. Text-fig. 22 uses Schmidt-Kittler's (1977*a*: text-fig. 11) and Louis & Sudre's (1975: 824, tab. 7) data and adds new material from Creechbarrow and the Hordle Cliff Mammal Bed (the latter mainly in R. Gardner's private collection).

M37148 is slightly larger than either of the Grisolles M^2s or that from Weissenburg 8. It resembles *P. crusafonti* in morphology except for the absence of pre- and post-metaconule cristae. At first sight this seems a relatively insignificant difference, but in all the upper molars of *P. parvulus* available from the Hordle Cliff Mammal Bed, presence of such cristae is constant.

Oddly, M35726 plots close to *P. reguanti* for size, the Weissenburg 8 tooth being larger and the *P. crusafonti* M_2 being smaller. From the pattern encountered in Recent *Tarsius* (p. 247) and Eocene *Microchoerus* (p. 260), M_{1-2} are more variable than M^{1-2} in size. Thus it need not be doubted that the type *P. crusafonti* assemblage is homogeneous. More material is needed from all localities for numerical and morphological variation to be evaluated, before definite identification of non-type material can be made.



Text-figure 22 Scatter diagrams of length (l) against width (w) in M_2 and M^2 of species of *Pseudoloris* from various European localities: ● = Hordle Cliff Mammal Bed; ◇ = Creechbarrow; ○ = Weissenburg 8; □ = type assemblage of *P. crusafonti* Louis & Sudre from Grisolles; △ = Perrière; ▲ = Le Bretou; ■ = Malpérié; ◆ = holotype of *P. reguanti* Crusafont-Pairo from San Cugat de Gavadons; ▽ = Eclépens [B]; ▼ = Nordshausen bei Kassel. Data from Weissenburg 8, San Cugat, Eclépens and Nordshausen from Schmidt-Kittler (1977*a*: text-fig. 11); those from Grisolles, Perrière, Le Bretou and Malpérié from Louis & Sudre (1975: tab. 7). Measurements in millimetres.

Genus *MICROCHOERUS* Wood 1844

TYPE SPECIES. *Microchoerus erinaceus* Wood 1844. Lower Headon Beds (early Ludian), Hordle Cliff, England.

INCLUDED SPECIES. *M. edwardsi* (Filhol 1880*a*); *M. ornatus* Stehlin 1916 (doubtfully distinct from *M. edwardsi*); *M. wardi* sp. nov.; *M. creechbarrowensis* sp. nov.; *M.* sp. from Grisolles.

RANGE. Bartonian (Marinesian) to late Ludian, England, France, West Germany, Switzerland and Spain.

EMENDED DIAGNOSIS. Tooth enamel wrinkling present; mesiolingual crest from paracone on I^1–P^4 present; P^{3-4} paracone–protocone crest may be present; P^4 metastylar wing short; upper molar *Nannopithex* fold present; M^{1-2} outline subquadrate, slightly broader than long to equidimensional; M^{1-2} hypocone nearly as large as protocone; M^{1-2} paraconule and metaconule large and metaconule double; M^{1-2} mesostyle present; I_1 broad with distolingual cingulum strong; P_{2-3} relatively moderately short with high distal cingula; M_1 trigonid length greater than talonid; M_{1-2} protocristid broken and displaced; M_{1-2} entoconid lower than metaconid; M_{1-2} hypoconulid small to large, single to double; M_3 hypoconulid lobe broad, moderately long to long, bicuspid; lower molar paracristid with paraconid on M_1, without paraconid and fusing with metaconid on M_{2-3}; angular process expanded; coronoid process low.

DIFFERENTIAL DIAGNOSIS. *Necrolemur* has no M^{1-2} mesostyle, small or absent M_{1-2} hypoconulid, smaller M^{1-2} paraconule and metaconule; and M_{1-2} protocristid is straight and complete to slightly broken and displaced and $M\frac{3}{3}$ are smaller with M_3 hypoconulid lobe usually shorter and narrower.

EVOLUTIONARY GRADE IN *Microchoerus*. Louis & Sudre (1975: 819–821) described the first recorded as well as the oldest known association of *Microchoerus* and *Necrolemur* at the same locality. They listed features which for them distinguished the two genera. They stated that a mesostyle is only sometimes present on *Microchoerus* upper molars, in contrast to most authors (e.g. Cooper 1910, Stehlin 1916, Hill 1955, Cray 1973, Schmid 1979) who have used it as a constant diagnostic feature. Study of the sample of *Microchoerus* from Grisolles in the UM has shown that, although variable in size and often weak, the mesostyle is constantly present even in this early (Marinesian) assemblage. Godinot (1985) has, however, recently documented a Ludian *Microchoerus* lineage in which the mesostyle is sometimes absent. Another character mentioned by Louis & Sudre was the greater lingual spread of the molar paracone and metacone in *Necrolemur*. Although difficult to assess, this seems to result from the smaller size of the paraconule and metaconule (the latter usually doubled) in *Necrolemur*. An examination of the occlusal relations of the upper and lower molars of *Necrolemur* and *Microchoerus* has shown that this, along with the remaining characters listed by Louis & Sudre, constitute important grade features which, however, could not entirely separate the two genera unless they occurred in association at the same locality.

These grade changes are outlined below; in each case the equivalent changes in the upper and lower teeth are placed alongside. For simplicity they are divided into two regions of the tooth: mesial and distal.

A. Mesial: M^{1-2}	M_{1-2}
1. Small paraconule, single paracone	Protocristid straight and unbroken.
2. Large paraconule, paracone single or incipiently double joined by crest.	Protocristid broken in middle, lingual half more distal than buccal half and may be confluent with cristid obliqua.
3. Large paraconule, double paracone.	Protocristid broken in middle, lingual half more distal than buccal half and may be confluent with cristid obliqua; mesoconid development on cristid obliqua.

B. Distal: M^{1-2}	M_{1-2}
1. Small metaconule, single or doubled.	Postcristid high, complete and even, without hypoconulid.
2. Large buccal metaconule and small lingual metaconule.	Postcristid lower, bent in middle just buccal to small hypoconulid.
3. Both metaconules large.	Postcristid broken by larger doubled hypoconulids.

Necrolemur zitteli is essentially at stage 1; *N. antiquus* may reach stage 2 (see also Godinot 1985); *Microchoerus erinaceus* is at stage 2 with some individuals tending towards stage 3; *M. edwardsi* has most individuals at stage 3; *M. ornatus* is at stage 3; *M. wardi* (p. 259) is at stage 2, with some tendency towards stage 3; *M. creechbarrowensis* (p. 261) is at stage 2; and *M.* sp. from Grisolles is between stages 1 and 2.

These characters indicate slight overlap in grade between late (Ludian) *Necrolemur* (*N. antiquus*) and early (Marinesian) *Microchoerus* (*M.* sp. from Grisolles). Only the presence of a mesostyle in *Microchoerus* then totally distinguishes it from *Necrolemur*. In those from Grisolles, it is a very weak structure. The evolution of *Microchoerus* from an animal with *Necrolemur*-

Table 7 Length (l) and maximum width (w) measurements of *Microchoerus* species from Creechbarrow. Measurements in millimetres.

	Microchoerus wardi			*Microchoerus creechbarrowensis*		
Tooth	No.	l	w	No.	l	w
C^1	M37159	2·00	1·80	M35428	(2·70)	1·85
	M37160	2·15	1·60	M35730	2·50	1·75
	M35742	2·30	1·60			
P^3	M35745	2·20	2·40			
P^4				M37155	2·60	3·20
M^1	M35436	2·90	3·40	M35731	3·25	(4·10)
	M35746	2·70	3·25	M35732	3·30	4·10
	M37162	2·65	3·25			
M^2	M35437	2·60	3·45	M35733	3·00	3·90
M^3	M37163	2·05	2·75	M35734	2·55	3·45
				M37156	2·50	3·00
I_1	M35747	1·70	1·65			
DI_1?	M35719	1·30	1·05			
P_2	M35439	2·25	1·55			
P_4	M35432	2·50	2·00	M37157	2·85	2·50
				M35431	2·95	2·10
				M37158	2·85	2·25
M_1	M35749	2·95	2·20			
	M37165	3·05	2·40			
M_2	M37166	2·95	2·30	M35737	3·25	2·60
	M35750	2·90	2·05			
$M_{1/2}$	M37167	–	2·15	M35739	–	(2·45)
M_3	M35752	–	1·90	M35433	–	2·55
	M35751	–	1·95			
	M35753	–	1·85			

like M^{1-2} is likely to have involved an increase in size accompanied by incipient development of a mesostyle and a molar grade change from 1 towards 2.

The species of *Microchoerus*. There has long been disagreement on how best to divide the genus at species level or lower, and on what criteria. *M. erinaceus* and *M. edwardsi* have been distinguished by some on size (e.g. Depéret 1917, Insole 1972) and others on degree of complication of tooth enamel by wrinkling and duplication of cusps (e.g. Stehlin 1916, Hill 1955, Cray 1973, Schmidt-Kittler 1971*b*, Louis & Sudre 1975, Schmidt-Kittler 1977*a*, Schmid 1979). In the latter case, *M. edwardsi* has often been reduced to the rank of a subspecies of *M. erinaceus*, because of overlap in the variable characters which define it for these authors. Insole (1972) considered that two distinct size groups occurred together through much of the Fluviomarine series (Ludian) of the Isle of Wight. On the basis of measurements of the type specimens, he attributed the larger one to *M. erinaceus*, the smaller to *M. edwardsi*. He considered *M. ornatus* to represent merely a variant of *M. edwardsi* in which enamel complication was extreme. At most horizons the sample sizes were low for at least one of the two species represented; but whereas the smaller form normally showed a duplicated molar paracone, the larger normally showed a single paracone (Insole 1972, text-figs 43–44, tab. 19).

This then suggested that Schmidt-Kittler's (1971*b*) evolutionary series of *M. erinaceus erinaceus* to *M. erinaceus edwardsi* was untenable, and that various small specimens from continental Europe attributed to *M. erinaceus*, or aff. or cf. to this species, have probably been misidentified. Insole's scatter diagrams also suggest that the same two size types of *Microchoerus* may have existed in continental Europe during the Ludian, but the sample sizes are very small. Further support, however, comes from rather large ranges of size and possible bimodality in some of Schmid's histograms (1979: 309, fig. 5), for instance 'Euzet/Perrière'. In this example, of course, the variation could alternatively have been increased by lumping two assemblages of slightly different ages. The coefficient of variation of Schmidt-Kittler's (1971*b*) M_1 length measurements from his *M. erinaceus edwardsi* assemblage from Ehrenstein 1A is greater than 10. Perhaps the smaller measurements belong to *Necrolemur* or a similar-sized undescribed species of *Microchoerus*.

The sample of *Microchoerus* teeth from the English Bartonian (Creechbarrow) is small, but two sizes appear to be represented. One is the size of *M. edwardsi*, the other is smaller. The M^{1-2} plot of *Microchoerus* from Grisolles, according to Louis & Sudre's (1975) measurements, is intermediate between the two from Creechbarrow (Text-fig. 23A). It is considered that, despite the small number of specimens, two species are represented at Creechbarrow, because both of the distance of size separation, and of the total size range spanned by the two (coefficient of variation of M^1 is greater than 10). They both also differ from *M. erinaceus*, *M. edwardsi* and the undescribed species from Grisolles.

Microchoerus wardi sp. nov.
(Pl. 6, figs 2–3; Pl. 7; Text-fig. 23; Tables 7–8)

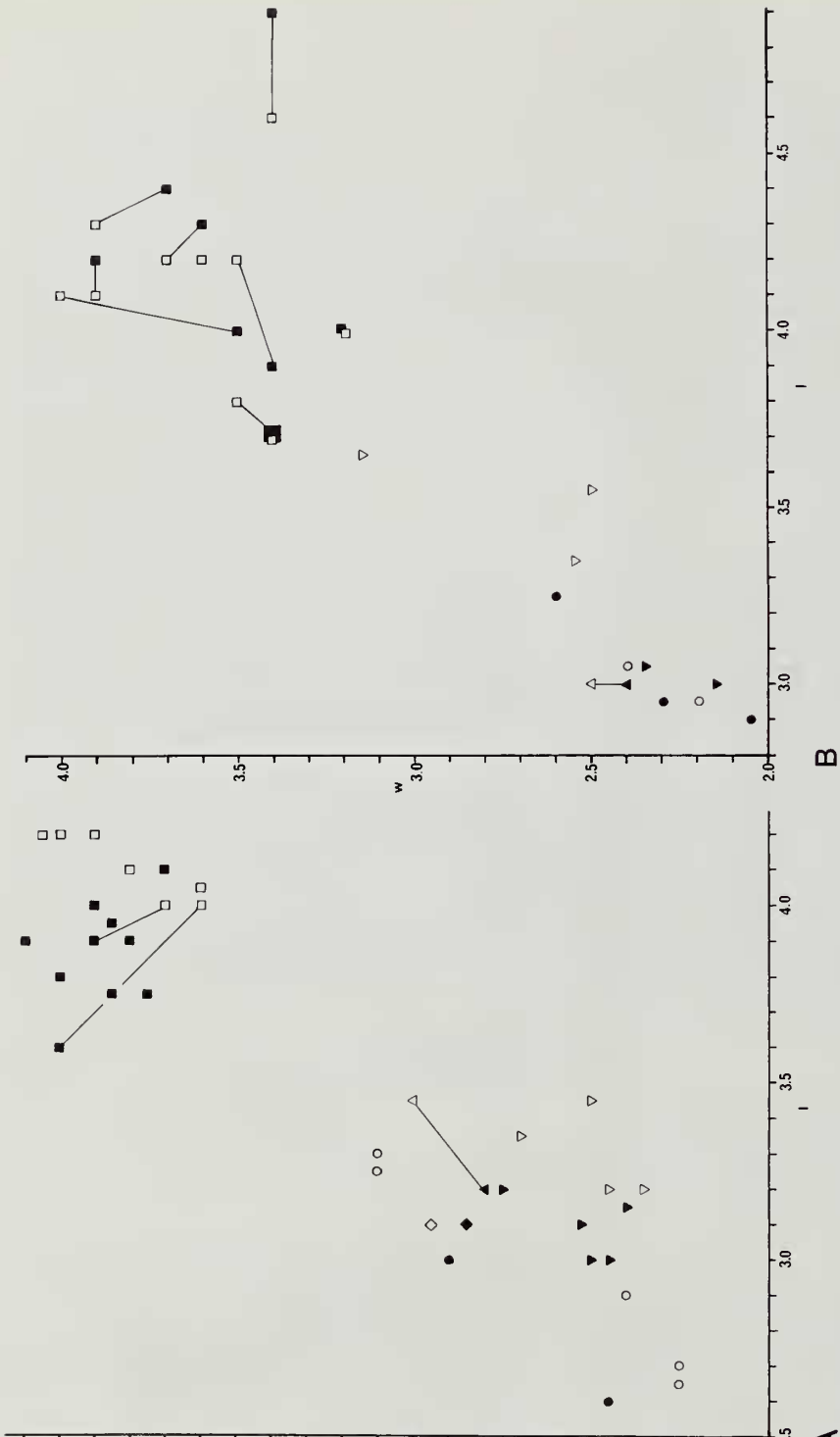
vp. *1977b Microchoerus* sp.; Hooker: 141.
v. *1980 Microchoerus* sp. 1; Hooker & Insole: 38.

Name. After Mr D. J. and Mrs A. Ward, for help with field work.

Holotype. Right M^1, M37162. Pl. 7, fig. 4.

Paratypes. Two left upper canines (M37159–60); right upper canine (M35742); right P^3 (M35745); right P^4 protoconal fragment (M35743); two complete right M^1s and one fragment (M35436, M35746, M35435); right M^2 (M35437); left M^3 (M37163); left I_1 with tip broken (M35747); left DI_1? (M35719); right P_2 (M35439); right P_4 (M35432); left M_1 (M35749); right M_1 (M37165); left M_2 (M37166); right M_2 (M35750); right $M_{1/2}$ talonid fragment (M37167); left $M_{1/2}$ buccal fragment (M37168); three right M_3s, one lacking much of the talonid (M35752), the other two lacking the trigonid (M35751, M35753).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.



Text-figure 23 Scatter diagram of length (l) against width (w) of M^{1-2} (A) and M_{1-2} (B) of species of *Microchoerus* from various European localities: ○ = Creechbarrow (*M. wardi* and *M. creechbarrowensis* spp. nov.); □ = Lower Headon Beds, Hordle Cliff (*M. erinaceus* Wood); ◇ = Lower Headon Beds, Headon Hill (*M. edwardsi?*); ▽ = Grisolles; △ = Holotype *M. ornatus* Stehlin from Entreroches in diagram A and holotype of *M. edwardsi* (Filhol) from Quercy in diagram B. Outline symbol = $M^{\frac{1}{1}}$, solid symbol = $M^{\frac{2}{2}}$. Data for Hordle Cliff from Cray (1973), for Headon Hill from Insole (1972), for Grisolles from Louis & Sudre (1975), for Entreroches from Stehlin (1916) and for Quercy from Filhol (1880*a*). Measurements in millimetres. Lines join teeth of one individual.

DIAGNOSIS. Size small ($\bar{x}$ M^1 length = 2·75 mm). Lingual M^{1-2} metaconule usually cuspate, smaller than the buccal metaconule. Strong M^{1-2} mesostyle small to medium. Upper molar paracone sometimes double. M_{1-2} protocristid variable. M_{1-2} postcristid complete, high to slow, slightly to strongly bent in middle. M_{1-2} hypoconulid single, small to large. M_3 hypoconulid lobe nearly as large as talonid.

DESCRIPTION. The upper canine is typical for the genus in having the mesiolingual paracone crest, enclosing a triangular mesial hollow between it and the preparacrista.

The P^3 and P^4 are typical and the enamel is more wrinkled than in the *M. creechbarrowensis* P^4.

Selected important characters of M^{1-2} (other than mesostyle morphology) are indicated in Table 8 in comparison with other *Microchoerus* assemblages. The mesostyle is equidistant between paracone and metacone except on M35746, where it is slightly more distal in position and curves distally where it meets the ectocingulum, there being an ectoflexus immediately mesially. This latter specimen is more like the two M^1s of *M. creechbarrowensis*. In M35436–7 and M37162 the mesostyle is straight, forming a broad ridge which reaches or nearly reaches the ectocingulum from the median point of the centrocrista. The mesostyle on the Grisolles M^{1-2}s is generally weaker (see Table 8) but similarly ridge-like. This ridge-like shape was characterized as the most basic type of *Microchoerus* mesostyle by Schmidt-Kittler (1971*b*: 187; 'Transversalgrates'). His other two more advanced types were: looped ('Mesostyl-Schleife') and conical ('spitz-kegelförmiges'). The last two do not occur in the Creechbarrow or Grisolles assemblages as at present known, but they do occur in *M. erinaceus* from the Lower Headon Beds of Hordle Cliff.

The M^3 is broader than long with the talon only slightly expanded distal to the hypocone. The paracone is double. A small mesostyle arises from the ectocingulum and is joined by a faint ridge to a point on the centrocrista distal of the midline.

I_1 lacks the weak buccal cingulum present in two specimens of *M. erinaceus* from Hordle Cliff. The morphology is otherwise identical.

The DI_1? is very similar in overall morphology to I_1 but is much smaller, has a faint rib on the buccal wall, a faint mesiobuccal cingulum, a small talonid cusp and thinner enamel.

The P_4 fits Teilhard's (1921: text-fig. 5A) normal ('nonmolariform') type, with small median paraconid and near longitudinal paracristid. The metaconid is distinctly smaller than the protoconid and is bounded by a lingual cingulum.

For M_{1-2} see Table 8. Both the M_3s (M35751 and M35753) have a bicuspid hypoconulid lobe, which is shorter and broader in the latter than in the former. They have been compared with ten M_3s of *M. erinaceus* (including the holotype) from the Lower Headon Beds of Hordle Cliff; in all of these the lobe is narrower than in M35753. Also the distance between the entoconid and lingual hypoconulid is always less than that between the entoconid and hypoconid. Only two Hordle Cliff specimens are like M35753 in having the former distance almost as great as the latter. In M35751, the lingual hypoconulid is further away from the entoconid than is the hypoconid. Thus in length and width of the hypoconulid lobe, *M. wardi* is more like *M. edwardsi* (e.g. see Schmidt-Kittler 1971*b*: pl. 13, fig. 3; 1977*a*: 189, text-fig. 9a) than *M. erinaceus* (see Cray 1973: pl. 3, fig. 1; pl. 4, fig. 1).

Microchoerus creechbarrowensis sp. nov.
(Pl. 8; Text-fig. 23; Tables 7–8)

vp. *1977b* *Microchoerus* sp.; Hooker: 141.
v. *1980* *Microchoerus* sp. 2; Hooker & Insole: 38.

NAME. From the type locality.

HOLOTYPE. Right M^1, M35732. Pl. 8, fig. 2.

PARATYPES. Two right upper canines (M35428, M35730); left P^4 (M37155); right M^1 (M35731); right M^2 (M35733); three right M^3s, the third one fragmentary (M35734, M37156, M35735);

6

7

11

5

1

10

4

9

2

3

8

two left P_4s (M35430, M37157); two right P_4s (M35431, M37158); left M_2 (M35737); two right $M_{1/2}$ talonid fragments (M35738–9); left M_3 (M35433).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Size medium ($\bar{x}$ M^1 length = 3·28 mm). Lingual M^{1-2} metaconule more often a transverse ridge, than a cusp smaller than the buccal metaconule. Strong M^{1-2} mesostyle medium to large. Upper molar paracone single. M_2 protocristid unbroken. M_{1-2} postcristid high, complete, slightly broken in middle. M_{1-2} hypoconulid single, usually small. [M_3 hypoconulid lobe unknown].

DESCRIPTION. On P^4 the enamel is very weakly wrinkled; there is no hypocone but instead a small hypostyle.

Selected important characters (other than mesostyle morphology) are listed in Table 8. On both M^1s the ectocingulum is raised into a large mesostylar cusp just mesiobuccal to the metacone; a crest from its mesial end joins it to the centrocrista just distal to the midpoint. This form of mesostyle was not described by Schmidt-Kittler (1971*b*) for *M. edwardsi* from Ehrenstein 1A and does not occur in the assemblages from Grisolles or Hordle Cliff. More specimens are needed to tell whether this character has more than individual importance in the light of the wide intraspecific morphological variation usually encountered in this genus. Both specimens are too worn to compare enamel wrinkling with that of *M. wardi*. The M^2 mesostyle is a more normal transverse ridge occurring only slightly distal to the centrocrista midpoint.

One M^3 (M35734) is nearly twice as broad as long and talon expansion is similar to *M. wardi*. There is a weak distal ridge-like mesostyle. M37156, conversely, is nearly as long as broad with a much more expanded talon and the paracone and metacone are more separated than on M35734. There is no mesostyle. On both teeth the paracone is single.

Of the three complete P_4s, M37157 is like Teilhard's (1921: text-fig. 5A) normal (non-molariform) type, like *M. wardi* but without the lingual cingulum and with subequal protoconid and metaconid; whereas M35431 and M37158 are of his molarized type (1921: text-fig. 5B) with larger lingual paraconid. Paraconid and metaconid are not fused, however, as they are in Teilhard's extreme example.

For M_{1-2} see Table 8. The M_3 has its hypoconulid lobe missing. Its enamel is less wrinkled than in *M. wardi* M_3s.

PHYLOGENY OF *Microchoerus*. Insole's (1972) view of large *M. erinaceus* and small *M. edwardsi* (including *M. ornatus*) evolving in parallel through the Ludian (discussed above) is considered a more plausible working hypothesis than that of Schmidt-Kittler (1971*b*), for whom these taxa had an ancestor–descendant relationship. Of the two Creechbarrow species, the smaller *M. wardi* is more like *M. edwardsi* in the upper molar paracone and M_3 hypoconulid lobe; whereas *M. creechbarrowensis* is more like *M. erinaceus* in the upper molar paracone. Moreover, there is slight evidence that there was greater percentage tooth enamel wrinkling in *M. wardi* than in *M. creechbarrowensis*, as in *M. edwardsi* over *M. erinaceus*.

It is possible that *M. wardi* and *M. creechbarrowensis* gave rise to *M. edwardsi* and *M. erinaceus* respectively, by size increase and the relevant grade change as discussed above. It is also possible that the *Microchoerus* from Grisolles, the most primitive of any described, gave rise to both *M. wardi* and *M. creechbarrowensis*. Whereas biostratigraphical evidence from

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Plate 7 Scanning electron micrographs of occlusal views of teeth of *Microchoerus wardi* sp. nov. from Creechbarrow, ×15. Fig. 1, right upper canine (reversed) (M35742). Fig. 2, right P^3 (reversed) (M35745). Fig. 3, lingual half of right P^4 (reversed) (M35743). Fig. 4, **holotype** right M^1 (reversed) (M37162). Fig. 5, right M^2 (reversed) (M35437). Fig. 6, left M^3 (M37163). Fig. 7, right P_2 (reversed) (M35439). Fig. 8, right P_4 (reversed) (M35432). Fig. 9, left M_1 (M35749). Fig. 10, right M_2 (reversed) (M35750). Fig. 11, right M_3 lacking trigonid (reversed) (M35751). See p. 259.

other mammalian groups places both Creechbarrow and Grisolles in the Marinesian, there is no independent stratigraphical evidence on the relative position of these sites within this time period (see correlation section). The scheme in Text-fig. 25 is provisional, based on the characters observed and as far as possible on stratigraphical position.

Table 8 Number rated development states of certain variable characters of $M\frac{1}{1}-\frac{2}{2}$ of species of *Microchoerus*.

Upper molars: Mesostyle size 1, 2, 3, 4. Paracone single or double: 1, 2. Hypostyle present or absent: 0, 1. Lingual metaconule: a transverse ridge (1); smaller than buccal metaconule (2); subequal with buccal metaconule (3). Pericone present or absent: 0, 1.

Lower molars: Protocristid broken lingual half: joined to cristid obliqua (1); separate from cristid obliqua (2). Mesoconid: absent (0); one small (1); one large, not separated from hypoconid (2); two or one very large separated from hypoconid (3). Postcristid: high, complete, slightly bent in middle (1); low complete, strongly bent in middle (2); low, incomplete (3); deeply divided (4). Hypoconulid: absent (0); one small (1); one large, distinct (2); two (3).

The presence of a hypoconulid or a mesoconid is somewhat arbitrary. Enamel wrinkles in the position of these cusps, no larger than those occurring on other parts of the tooth, are not considered to constitute presence of these cusps.

Tooth	Species and Locality	No.	Mesostyle size	Paracone	Hypostyle	Lingual metaconule	Pericone	Protostyle
M^1	*M.* sp.,		1	1	0	1	1	0
	Grisolles		1	1	1	1	0	–
			1	1	0	2	1	0
			2	1	0	1	1	0
M^2			1	1	0	–	0	0
			2	1	0	1	0	0
			2	1	0	1	0	0
M^1	*M. wardi*,	M37162	2	1	1	2	0	0
	Creechbarrow	M35746	3	1	1	1	1	0
		M35436	2	1	–	2	0	0
M^2		M35437	3	2	0	2	0	0
M^1	*M. creechbarrowensis*,	M35732	4	1	1	2	1	0
	Creechbarrow	M35731	4	1	1	1	1	0
M^2		M35733	3	–	0	1	0	0
M^1	*M. erinaceus*,	M34692	–	1	1	2	0	0
	Hordle Cliff	M34694	–	–	1	2	0	0
		M34693	2	1	1	2	1	0
		M34695	3	1	1	2	0	0
		M34810	–	–	1	2	0	0
		M35038	2	1	1	2	0	1
		30346b	3	1	1	2	0	0
		30346be	2	1	1	2	0	0
		25229	3	1	?1	1	1	0
M^2		M34696	3	1	1	2	0	1
		M34698	3	1	1	2	0	0
		M34699	3	1	0	2	1	0
		M34839	3	1	1	2	0	0
		M34840	–	1	1	2	0	0
		M34811	–	–	1	2	0	0
		M34760	3	1	1	2	0	–
		M34763	2	1	–	–	–	–
		M34688	–	1	1	2	1	0
		30346b	3	1	1	2	0	0
		25229	3	?1	1	2	1	0
	M. edwardsi,							
	La Débruge	M43059	3	1	2	3	0	0
M^1	*M. ornatus*,		–	2	1	3	0	0
M^2	Entreroches (Holotype)		4	2	2	3	0	0

PHYLOGENY WITHIN THE MICROCHOERINAE. Prior to Simons' (1961) study, the genera included in the Microchoerinae were thought to be sufficiently distantly related to be placed in different subfamilies. Hürzeler (1948*b*) considered *Nannopithex* to be either lateral to *Necrolemur* or a direct ancestor and a stage in the *Necrolemur* lineage. Russell *et al.* (1967: 17) considered that *Pseudoloris* on the other hand had certain tooth characters more like some adapids than like *Necrolemur*. Szalay (1975: fig. 2) showed *Nannopithex* as a stem genus, giving rise to *Pseudoloris* and independently to *Necrolemur* and *Microchoerus* (which were included together). The

Table 8 (*continued*)

Tooth	Species and Locality	No.	Protocristid	Mesoconid	Postcristid	Hypoconulid
M_1	*M.* sp.,		1	0	1	0
	Grisolles		1	0	1	1
			1	0	1	1
M_2			2	0	1	0
			2	0	1	1
M_1	*M. wardi*,	M35749	2	1	1	1
	Creechbarrow	M37165	2	1	1	1
M_2		M35750	0	1	2	2
		M37166	2	0	?2	2
$M_{1/2}$		M37168	?1	0	–	–
		M37167	–	?1	2	2
M_2	*M. creechbarrowensis*,	M35737	0	0	1	1
$M_{1/2}$	Creechbarrow	M35738	–	–	1	1
		M35739	–	–	1	2
M_1	*M. erinaceus*,	25229	–	2	–	3
	Hordle Cliff	30346b	2	1	–	–
		30346b	2	1	3	3
		30346b	2	?1	2	?3
		M35036	2	0	2	2
		M12565	2	2	3	3
		M12563	2	2	3	3
		30338	2	0	1	1
		30346	2	2	2	3
		M34816	2	2	3	2
		M34704	2	1	2	2
		M34714	2	2	3	2
		M34717	2	2	2	2
M_2		25229	–	1	–	2
		30346b	2	1	3	3
		30346b	2	1	2	3
		M35037	2	0	3	3
		M12565	2	2	3	3
		M12563	2	2	3	3
		30346	2	1	2	2
		M34830	0	0	2	3
		M34705	2	1	2	2
		M34707	2	1	3	2
		M34708	0	0	2	2
		M34712	2	2	3	3
		M34713	2	1	2	2
		M34714	2	1	3	2
		M34716	2	1	2	2
		M34717	2	1	2	2
$M_{1/2}$		M34817	–	–	3	3
M_1	*M. edwardsi*,	Qu10946	–	3	3	3
M_2	Quercy	Qu10946	2	3	4	3

Plate 8 Scanning electron micrographs of occlusal views of teeth of *Microchoerus creechbarrowensis* sp. nov. from Creechbarrow, × 15. Fig. 1, left P^4 (M37155). Fig. 2, **holotype** right M^1 (reversed) (M35732). Fig. 3, right M^2 (reversed) (M35733). Fig. 4, right M^3 (reversed) (M35734). Fig. 5, left P_4 (M35431). Fig. 6, left M_2 (M35737). Fig. 7, left M_3 lacking hypoconulid lobe (M35433). See p. 261.

characters given above in the diagnoses for the different genera suggest that *Necrolemur* and *Microchoerus* differentiated at a later time than did *Pseudoloris*. Perhaps *Pivetonia isabenae*, if distinct from *Nannopithex*, was connected with the derivation of *Pseudoloris*.

Simons (1961: 62–63) stated: 'At present specimens of *Nannopithex* have been recovered near Egerkingen in Switzerland, at Buchsweiler in Alsace, and in the Geisel valley near Halle, Germany. *Nannopithex* does not occur in the Quercy phosphorites of Bartonian and Ludian age. Its absence at this later period reinforces the idea based on morphology that a species of this genus could have given rise to *Necrolemur*'. The Creechbarrow records of two species of *Nannopithex* extend the range of the genus into the Bartonian, where it is associated with two species of *Microchoerus* and is contemporaneous with *Necrolemur*. This need not invalidate the evolutionary scheme envisaged. Some specimens of *Nannopithex filholi* from Egerkingen γ and the Huppersand (e.g Hürzeler 1948*b*: 17, fig. 8; 22, fig. 14) show characters overlapping slightly with *Necrolemur*. These characters are a larger M^1 hypocone and a bicuspid M_3 hypoconulid lobe. *Nannopithex*, with as many of its generic characters as are known, continues into the Bartonian with only minor differences from the Lutetian species. Although it is accepted that *Nannopithex* is paraphyletic, its concept as a microchoerine stem genus is a useful one and it is retained for this reason. See Table 9 and Text-figs 24–25 for character table, cladogram and phylogeny, where primitive versus advanced states have been calculated by outgroup comparison with the rest of the Omomyidae.

Infraorder **LEMURIFORMES** Gregory 1915

Family **ADAPIDAE** Trouessart 1879 (*sensu* Hill 1953)

Subfamily **ADAPINAE** Trouessart 1879
(nominate subfamily *sensu* Hill 1953)

TYPE GENUS. *Adapis* Cuvier 1822.

INCLUDED GENERA. *Donrussellia* Szalay 1976, *Pronycticebus* Grandidier 1904, *Protoadapis* Lemoine 1880, *Europolemur* Weigelt 1933, *Cercamonius* Gingerich 1975*c*, *Caenopithecus* Rütimeyer 1862, *Periconodon* Stehlin 1916, ?*Agerinia* Crusafont-Pairo & Golpe-Posse 1975 (= *Agerina* Crusafont-Pairo 1967), *Anchomomys* Stehlin 1916 (?including *Huerzeleris* Szalay 1974), *Microadapis* Szalay 1974, *Leptadapis* Gervais 1876, *Cryptadapis* Godinot 1984, *Mahgarita* Wilson & Szalay 1977 (= *Margarita* Wilson & Szalay 1976, *non* Leach 1814 &c.), *Indraloris* Lewis 1933 and *Sivaladapis* Gingerich & Sahni 1979.

RANGE. Sparnacian–Stampian, Europe; Uintan, U.S.A.; Late Miocene, India.

DIAGNOSIS. See Cray (1973: 65) under Adapidae.

Genus ***EUROPOLEMUR*** Weigelt 1933
[= *Megatarsius* Weigelt 1933 and *Alsatia* Tattersall & Schwartz 1984]

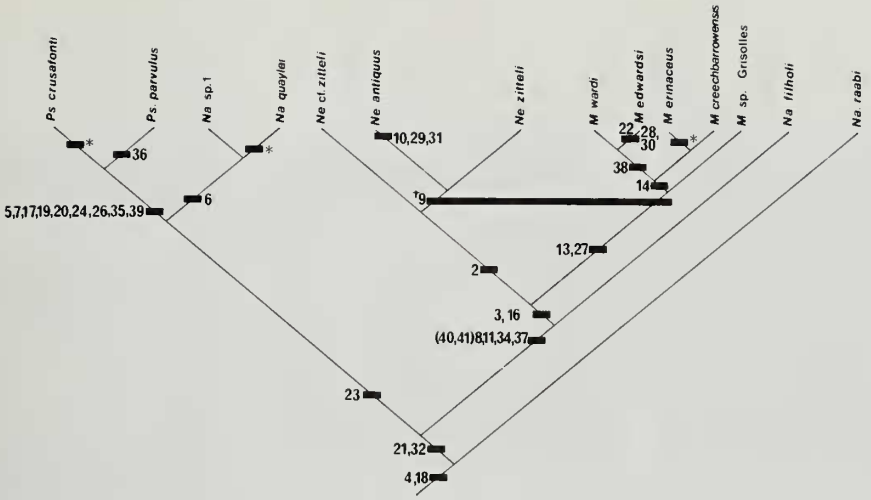
TYPE SPECIES. *E. klatti* Weigelt 1933. Lower Brown Coal, Leonhardt Mine, Geiseltal, D.D.R.

INCLUDED SPECIES. *E. collinsonae* sp. nov., *E.* aff. *klatti*.

RANGE. Early Lutetian, D.D.R.; Middle Lutetian, France; Late Lutetian, Switzerland; Bartonian, England.

EMENDED DIAGNOSIS. Medium to large adapine; dental formula $\frac{2\ 1\ 3\ 3}{2\ 1\ 3\ 3}$; canines large and pointed; upper molars without pericone or postflexus, with strong postprotocrista lacking metaconule; M^3 smaller and relatively shorter than M^2; P^4 much shorter than broad with weak parastyle; P_4 with small unicuspid talonid and metaconid present to absent; M_{1-2} protocristid and postcristid nearly transverse.

	Character	State: primitive	State: advanced	*Na. raabi*	*Na. filholi*	*Na. quaylei* and sp. 1	*Ps. parvulus*	*Ps. crusafonti*	*Ne.* cf. *zitteli*	*Ne. zitteli*	*Ne. antiquus*	*M.* sp. (Grisolles)	*M. wardi*	*M. creechbarrowensis*	*M. erinaceus*	*M. edwardsi*
1	Enamel wrinkling	no	yes	+/−	+	−	−	−	+	+	+	+	+	+	+	+
2	M3	not reduced	reduced	−	−	−	−	−	+	+	+	−	−	−	−	−
3	Mesiolingual paracone crest	no	yes	−	−	−	−	−	+	+	+	+	+	+	+	+
4	I^2 reduction	slight	great	+	?+	?+	+	?+	+	+	+	+	+	+	+	+
5	P^4 metastylar wing	short	long	−	−	−	+	+	−	−	−	−	−	−	−	−
6	P^4 parastyle	weak	strong	−	−	+	−	−	−	−	−	−	−	−	−	−
7	Upper molar *Nannopithex* fold	yes	no	−	−	−	+	+	−	−	−	−	−	−	−	−
8	M^{1-2} outline	subtriangular	subquadrate	−	+/−	−	−	−	+	+	+	+	+	+	+	+
9	M^1 width	>length	=length	−	−	−	−	−	−	+	+	+	+	+	+	+
10	M^{1-2} paraconule and metaconule	small	large	−	−	−	−	−	−	−	+/−	+/−	+	+	+	+
11	M^{1-2} metaconule	single	double	−	+/−	−	−	−	+/−	+/−	+/−	+	+	+	+	+
12	M^{1-2} paracone	single	double	−	−	−	−	−	−	−	+/−	−	+/−	−	+/−	+
13	M^{1-2} mesostyle	no	yes	−	−	−	−	−	−	−	−	+	+	+	+	+
14	Mesostyle strength	weak	strong									−	+	+	+	+
15	M^{1-2} hypocone	weak	strong	−	+/−	−	+	−	+	+	+	+	+	+	+	+
16	I_1 width	narrow	broad	−	?	−	−	?−	?+	+	+	+	+	?+	+	+
17	I_1 distolingual cingulum	strong	weak	−	?−	−	+	?+	−	−	−	−	−	?−	−	−
18	Lower canine reduction	slight	great	+	?+	?+	+	?+	?+	+	+	?+	?+	?+	+	+
19	P_{2-3} distal cingulum	high	low	−	−	−	+	?+	−	−	−	−	−	?−	−	−
20	P_{2-3} l/w proportions	c. 1	>1	−	−	−	+	?+	−	−	−	−	−	?−	−	−
21	P_3 roots	sometimes 2	always 1	−	+	+	+	?+	+	+	+	+	?+	?+	+	+
22	Lower molar mesoconid	no	yes	−	−	−	−	−	−	−	−	−	+/−	−	+/−	+
23	M_1 trigonid length	>talonid	=talonid	−	−	+	+	+	−	−	−	−	−	−	−	−
24	M_1 paraconid	yes	no	−	−	?−	+	+	−	−	−	−	−	−	−	−
25	M_2 paraconid	yes	no	−	+/−	?−	+	+	+	+	+	+	+	+	+	+
26	M_{1-2} entoconid height	<metaconid	=metaconid	−	−	?−	+	+	−	−	−	−	−	−	−	−
27	M_{1-2} hypoconulid	variable	constant	−	−	−	−	−	−	−	−	+	+	+	+	+
28	M_{1-2} hypoconulid	single	usually double	−	−	−	−	−	−	−	−	−	−	−	+/−	+
29	M_{1-2} postcristid	straight	bent in middle	−	−	−	−	−	−	−	+/−	+/−	+	+	+	+
30	M_{1-2} postcristid	unbroken	broken	−	−	−	−	−	−	−	−	−	−	−	+/−	+
31	M_{1-2} protocristid	straight	displaced	−	−	−	−	−	−	−	+/−	+/−	+	+	+	+
32	M_3 paraconid	maybe present	absent	−	+	?+	+	+	+	+	+	+	+	+	+	+
33	M_3 hypoconulid lobe	short	long	−	+/−	+	−	−	+/−	+/−	+/−	+	+	+	+	+
34	M_3 hypoconulid lobe	narrow	broad	−	+/−	−	−	−	+/−	+/−	+	+	+	+	+	+
35	M_3 hypoconulid lobe	unconstricted	constricted	−	−	−	+	+	−	−	−	−	−	−	−	−
36	M_3 hypoconulid constriction	weak	strong				+	−								
37	M_3 hypoconulid lobe	unicuspid	bicuspid	−	+/−	−	−	−	+/−	+	+	+	+	+	+	+
38	Broad hypoconulid lobe	not inflated	inflated		−				−	−	−	−	+	−	−	+
39	M_3 paracristid – metaconid	joined	not joined	−	−	?−	+	+	−	−	−	−	−	−	−	−
40	Angular process expansion	no	yes	−	?+	?	−	?−	?+	+	+	?+	?+	?+	+	+
41	Coronoid process	high	low	−	?+	?	+	?+	?+	+	+	?+	?+	?+	+	+



Text-figure 24 Cladogram of species of the omomyid subfamily Microchoerinae. This is probably one of the most parsimonious possibilities but has not been subjected to computer analysis. Some characters are unknown for a few species only (e.g. *Ps. crusafonti*, *Na. filholi*, *Na. quaylei*), whilst others are generally poorly known (e.g. 40, 41). For instance, characters 40 and 41 are known in most species of *Necrolemur* and *Microchoerus* but it is not known whether they were incipiently developed in *Na. filholi* like characters 8, 11, 34 and 37. *Na. filholi* appears to be very variable morphologically (see Hürzeler 1948*b*), some individuals differing little from *Na. raabi*, while others show marked trends towards *Necrolemur* and *Microchoerus*. At terminal or near terminal branchings, often only size (the larger indicated by *) or a parallelism (†) are available as advanced character states. The large number of characters separating *Pseudoloris* from the rest might indicate a more distant relationship for this genus or alternatively a lack of intermediates. The correct alternative might become apparent from a detailed study of all three omomyid subfamilies and a better knowledge of *Pivetonia*. Abbreviations: *M.* = *Microchoerus*; *Na.* = *Nannopithex*; *Ne.* = *Necrolemur*; *Pi.* = *Pivetonia*; and *Ps.* = *Pseudoloris*. Character numbers are identified in Table 9, opposite.

Differential diagnosis. *Protoadapis* differs in having M^{1-2} with small metaconules, P^4 with large parastyle and P_4 with constant metaconid.

Cercamonius has P_4 with metaconid and P_2 greatly reduced.

Mahgarita has M^{1-2} metaconule, $P\frac{2}{2}$ greatly reduced, P^3 with reduced protocone.

Pronycticebus and *Donrussellia* have large P^4 parastyle, transversely elongated M^{1-2} with metaconules and P_4 with metaconid and bicuspid talonid.

Periconodon has M^{1-2} metaconule and pericone and weak, distally placed P_4 metaconid.

Agerinia has strong P_4 metaconid and $P_3 = P_4$ in height.

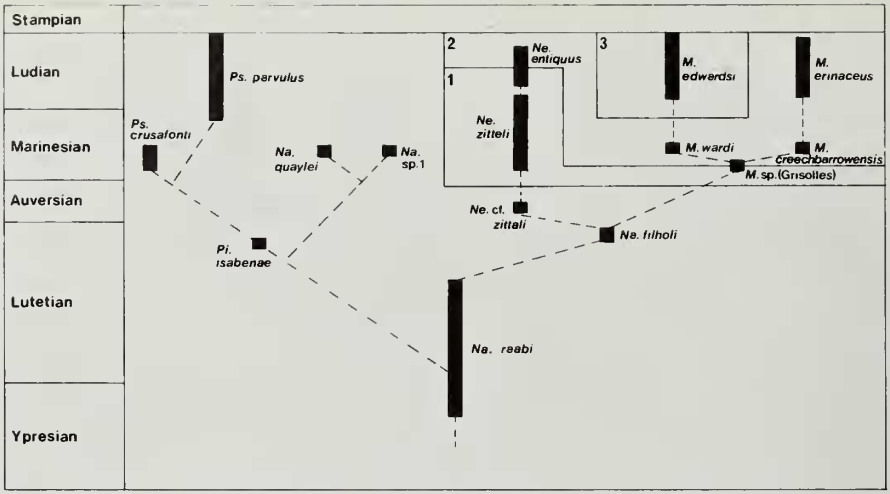
Anchomomys is smaller, has M^{1-2} postflexus and oblique protocristid and postcristid.

Microadapis has M^1 metaconule, P_4 metaconid.

Adapis, *Cryptadapis* and *Leptadapis* have weak M^{1-2} postprotocrista and nearly molariform $P\frac{4}{4}$.

Discussion. Weigelt (1933: 123) described the type species in detail but gave no formal generic diagnosis. Simons (1962: 12–14) revised the type species, placing it in *Protoadapis*, whose upper

Table 9 Characters and character states of species in the Microchoerinae. Characters are estimated as primitive (−) or advanced (+) based on outgroup comparison with the rest of the Omomyidae. '?' indicates lack of information on a character. *Na.* = *Nannopithex*; *Ps.* = *Pseudoloris*; *Ne.* = *Necrolemur*; *M.* = *Microchoerus*.



Text-figure 25 Phylogenetic model for Microchoerinae, derived from the cladogram in Text-fig. 24 (p. 269) and from stratigraphical occurrences. The numbers refer to the grades described for *Microchoerus* (p. 257) and also as they affect *Necrolemur*. Their limits are arbitrary as they exhibit gradual changes, and in some cases do not coincide with recognized species boundaries. In the case of *M.* sp. from Grisolles this is because the assemblage exhibits a grade intermediate between 1 and 2. In the case of *N. antiquus* Filhol, the change from *N. zitteli* Schlosser to *N. antiquus* reflects other changes; moreover, known specimens of *N. antiquus* are mainly from the old collections of the Quercy Phosphorites, involving mixed assemblages in which both grades 1 and 2 occur. For abbreviations see Text-fig. 24.

dentition was then unknown. Russell *et al.* (1967: 38) used absence of an M^1 ('M_1' in Russell *et al.* must be an error) metaconule as a specific character of '*P.*' *klatti*. Wilson & Szalay (1976) resurrected *Europolemur* for the type species.

Simons (1962: 12), Russell *et al.* (1967: 38) and Szalay & Delson (1979: 125) all quoted an M_{1-2} hypoconulid as a distinctive feature of *E. klatti*. The two available specimens with lower teeth lack this cusp, although there is a buccally oblique ridge running down the distal postcristid wall. Its absence has been omitted from the generic diagnosis herein because *E. collinsonae* does have a M_{1-2} hypoconulid.

The variable occurrence of a P_4 metaconid in *E. klatti* (present in Simons' (1962: pl. 3, fig. F), absent in Szalay & Delson's (1979: fig. 57B, D–E) figures) is considered to represent the beginning of an important trend in simplifying P_4, carried a stage further in *E. collinsonae* below.

With the description of the new species below, *Europolemur* is no longer monotypic, Gingerich's (1977*a*: 61) main reason for reuniting *E. klatti* with *Protoadapis*, and it is easier to understand the importance of its generic characters.

Europolemur collinsonae sp. nov.
(Pl. 9, figs 3–4; Pl. 10; Table 10)

v. *1977b* ?*Caenopithecus* sp.; Hooker: 141.
v. *1980* ?*Protoadapis* sp.; Hooker & Insole: 31, 38.

NAME. After Dr M. E. Collinson for her help with field work and other aspects of this project.

HOLOTYPE. Left M^2, M37169. Pl. 9, fig. 3.

PARATYPES. Left M^3 (M35440), right M^3 (M37170), left P_4 (M37171), two right M_1s with incomplete talonids (M35755, M37173), right M_2 (M35756), right $M_{1/2}$ talonid fragment (M37172), two left M_3s, one a trigonid fragment (M35757, M37693).

Plate 9 Light macrographs of upper molars of *Europolemur*, ×8. Figs 3a and 4a are buccal views, the rest occlusal.

Fig. 1 *Europolemur klatti* Weigelt from Bouxwiller, France. Cast of right M^2 (reversed) (NMB Bchs648; holotype of synonym, *Alsatia dunaifi* Tattersall & Schwartz 1984).

Fig. 2 *Europolemur* aff. *klatti* Weigelt from Egerkingen γ, Switzerland. Cast of right M^2 (reversed) (NMB unnumbered; BM(NH) cast no. M42083).

Figs 3, 4 *Europolemur collinsonae* sp. nov. from Creechbarrow. Fig. 3a, b, **holotype** left M^2 (M37169). Fig. 4a, b, right M^3 (reversed) (M37170). See opposite.

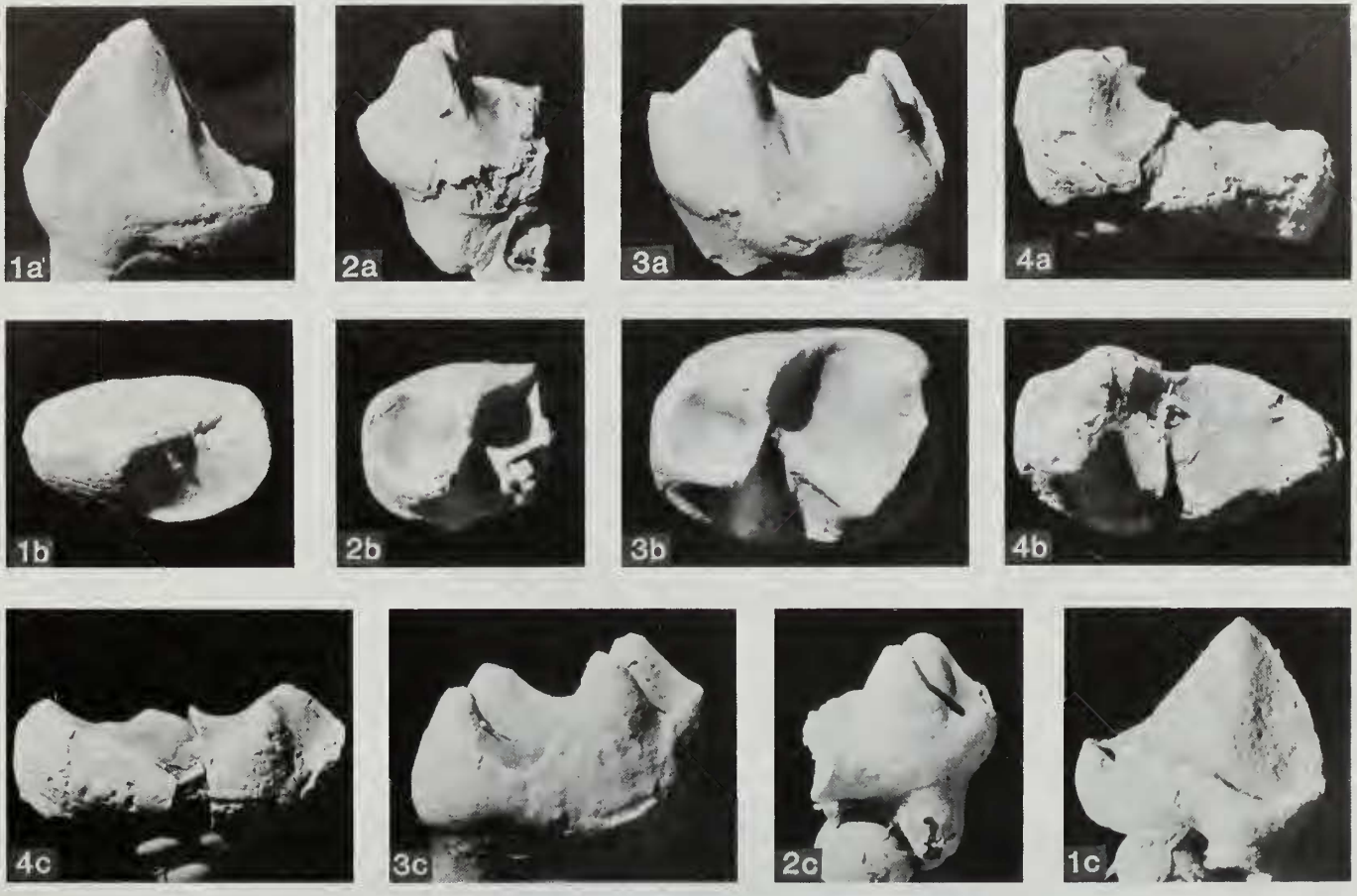


Plate 10 Light macrographs of lower cheek teeth of *Europolemur collinsonae* sp. nov. from Creechbarrow, ×8. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, left P_4 (M37171). Fig. 2a–c, right M_1 with incomplete talonid (reversed) (M35755). Fig. 3a–c, right M_2 (reversed) (M35756). Fig. 4a–c, left M_3 (M35757). See p. 270.

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Large *Europolemur* (M^2 length 4·9 mm); M^2 with hypocone nearly as tall as protocone, centrocrista buccally flexed, postprotocrista distally arched and metacone as far from paracone as is protocone; M^3 with small hypocone; P_4 with postprotocristid essentially straight, ending just short of distolingual corner, and without paraconid or metaconid; M_{1-2} with entoconid distal to and nearly as tall as hypoconid and with hypoconulid present.

DIFFERENTIAL DIAGNOSIS. *E. klatti* is slightly smaller, M^2 with smaller hypocone, straight centrocrista, only slightly distally arched postprotocrista and metacone closer to paracone than is protocone; M^3 lacks hypocone; P_4 with metaconid or with postprotocristid kinked at midpoint in position of absent metaconid and with very small paraconid; M_{1-2} with lower entoconid, which is transversely opposite hypoconid, and without hypoconulid.

DESCRIPTION. Because of the small number of specimens, documentation of variation is restricted to M^3, M_1 and M_3 (two specimens of each).

Of the M^3s, M37170 (Pl. 9, fig. 4) is broader lingually than M35440, which is triangular in shape, and its hypocone appears larger, although M35440 is more worn. The crown base of the hypocone is drawn out into a point lingually on M35440 over a transversely elongated and mesiodistally short lingual root.

M_1 can be distinguished from M_2 by having a longer trigonid which is angled instead of bevelled mesiolingually (Pl. 10, figs 2–3). There is no paraconid. On both M_1s the buccal cingulum is stronger than on the M_2, probably an individual difference.

The only complete M_3 (Pl. 10, fig. 4) is considerably worn but shows the presence of an entoconid smaller than the hypoconid. The tooth as a whole is narrower than the M_2 and is only very slightly larger than a topotype *E. klatti* M_3 (GH XXII/7-1961) (see Szalay & Delson 1979: 124, fig. 57B, D–E).

PHYLOGENY. A right M^2 (NMB unnumbered, cast in BM(NH) no. M42083) of *Europolemur* from Egerkingen γ is intermediate in morphology between *E. klatti* from Geiseltal and Bouxwiller and *E. collinsonae* from Creechbarrow. It is the same size as *E. klatti* but has a hypocone nearly as large as in *E. collinsonae*; its postprotocrista is slightly more distally arched than in *E. klatti*; the buccal flexing of its centrocrista is intermediate between the two species; and in the remaining characters it is similar to *E. klatti* (see Pl. 9, figs 1–3). It is thus best referred to as *E.* aff. *klatti*, but if more material should be found it may be shown to belong to a new species. It is also intermediate in time between *E. klatti* and *E. collinsonae* and it is likely that the three represent an evolving lineage. Some of the trends are similar to those which produced the

Table 10 Length (l) and mesial (w_1) and distal (w_2) width measurements of *Europolemur collinsonae* from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1	w_2
M37160	LM^2	4·9	6·2	
M35440	LM^3	4·2	(6·7)	
M37170	RM^3	4·1	6·1	
M37171	LP_4	4·2	2·5	
M35755	RM_1	–	(2·9)	–
M37173	RM_1	–	(2·8)	–
M35756	RM_2	5·1	3·5	3·7
M37172	$RM_{1/2}$	–	–	3·9
M35757	LM_3	5·6	3·0	2·9
M37693	LM_3	–	2·8	–

Lutetian *Caenopithecus*, with which *E. collinsonae* was first confused (Hooker 1977*b*). In particular, the buccal flexing of the centrocrista, unlike that of *Caenopithecus*, did not go as far as development of a mesostyle, nor did $M\frac{3}{3}$ expand, nor lower molar metastylids form. Instead the hypocone grew larger and the reduction of P_4 was different in aspect (Pl. 10, fig. 1), the metaconid being lost instead of being shifted lingually, and the protoconid remaining high. Both *Europolemur* and *Caenopithecus* probably share a common ancestry in *Protoadapis* (see Gingerich 1977*a*: 77, fig. 8).

Genus ***LEPTADAPIS*** Gervais 1876

[incl. *Paradapis* Tattersall & Schwartz 1984 and ?*Arisella* Crusafont-Pairo 1967]

TYPE SPECIES. *Adapis magnus* Filhol 1874. Phosphorites du Quercy, Raynal, France.

INCLUDED SPECIES. *L. ruetimeyeri* Stehlin 1912, *L. priscus* (Stehlin 1916) Szalay & Delson 1979, *L. stintoni* (Gingerich 1977*a*) Schwartz & Tattersall 1985, *L*? *capellae* (Crusafont-Pairo 1967) ?Szalay & Delson 1979.

RANGE. Bartonian–Stampian, England; ?Bartonian–late Ludian, France; late Lutetian–Auversian, Switzerland; ?Lutetian, Spain; Ludian, W. Germany.

EMENDED DIAGNOSIS. Medium to large adapine; dental formula $\frac{2\ 1\ 4\ 3}{2\ 1\ 4\ 3}$, canines large and pointed, uppers with apically converging ridges and grooves, lowers slightly procumbent; incisors and $P\frac{1}{1}$ reduced ($P\frac{1}{1}$ half the linear dimensions of $P\frac{2}{2}$); $P\frac{4}{4}$ semimolariform; upper molar postprotocrista weak and without metaconule; M_{1-2} hypoconulid median and postcristid slightly oblique; M_3 normally without entoconid; facial region of cranium nearly as high as long; mandibular ramus of approximately equal depth front to back.

DIFFERENTIAL DIAGNOSIS. *Microadapis* differs in having large hypocone and paraconule and metaconule on M^1 and large entoconid on M_3. *Cryptadapis* has slightly narrower lower cheek teeth and upper molars with slightly larger hypocone.

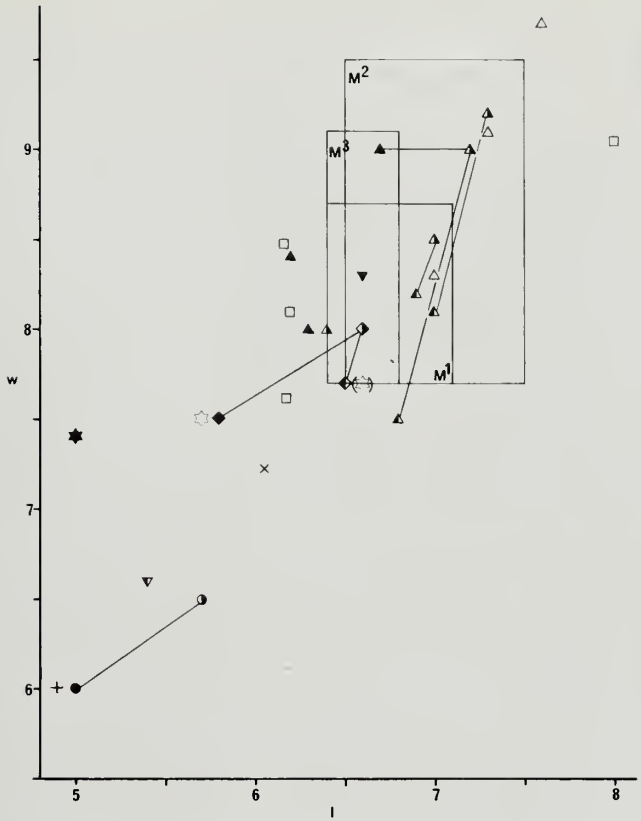
Adapis has smaller canines, the uppers ungrooved and buccolingually compressed, the lowers with a mesially sloping crested tip; incisors and $P\frac{1}{1}$ not reduced ($P\frac{1}{1}$ nearly as large as $P\frac{2}{2}$); M_{1-2} hypoconulid close to entoconid and postcristid strongly oblique; M_3 often with small sharp entoconid; facial region of cranium much lower than long; mandibular ramus deepening posteriorly.

All other adapines (where relevant parts are known) have strong upper molar postprotocrista and non-molariform $P\frac{4}{4}$.

DISCUSSION. *Leptadapis* has been used much less frequently as a genus for the species *L. magnus* than has *Adapis*, probably because it is evidently closely related and the number of species involved is small. Sometimes *Leptadapis* has been used as a subgenus of *Adapis* (e.g. Stehlin 1912; Gingerich 1975*b*). More recently Szalay (1974: 131–132) has supported separation of the two as genera, with a brief functional analysis of the slightly different anterior dentitions. Gingerich (1977*a*: 71–72, figs 2, 5) described *Adapis stintoni* as both a morphological and stratigraphical intermediate between *A. magnus* and *A. parisiensis*, thus providing reasons for synonymizing *Leptadapis* with *Adapis*. Gingerich (1977*b*, 1981) reiterated his view of the *A. magnus*→ *A. stintoni*→ *A. parisiensis* lineage but also noted (1977*b*: 171) a personal communication from Sudre that two sizes of *Adapis* occurred in the French locality of Pont d'Assou (Tarn), which if confirmed would thus contradict his evolutionary scheme.

An examination of the holotype (M32135) has shown that '*A.*' *stintoni* resembles referred *L. magnus* specimens in that its mandible is uniformly shallow from front to back, and in its large lower canine and small P_1 (judged from alveoli), almost transverse lower molar postcristids and mesial P_4 metaconid. It is thus here referred to *Leptadapis*. It should not be synonymized with *A. parisiensis* as Szalay & Delson (1979: 139) have done. (Note that while this paper was in press, Schwartz & Tattersall (1985: 92) also recombined '*A.*' *stintoni* with *Leptadapis*.)

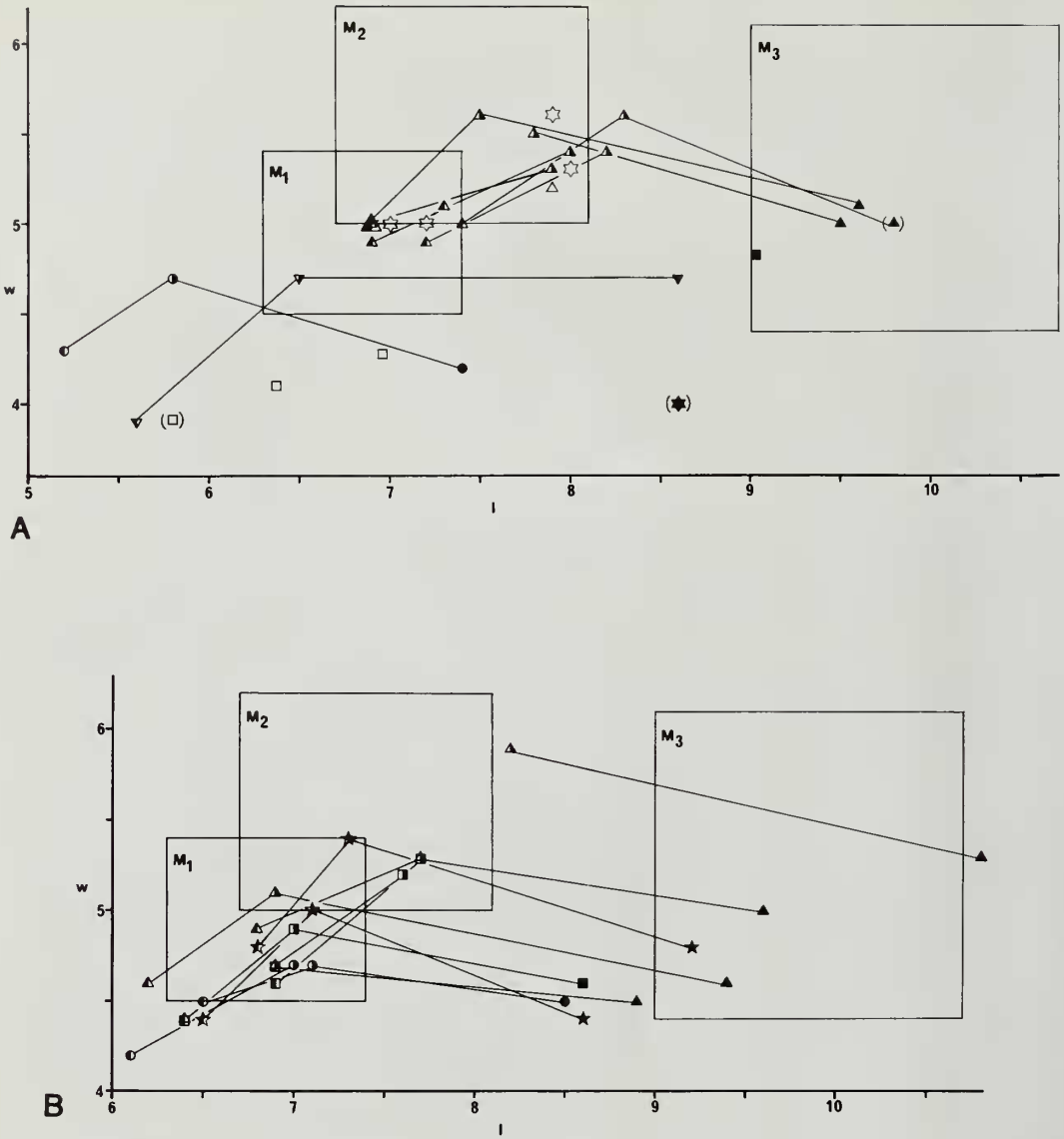
The realization that '*A.*' *stintoni* is in reality a *Leptadapis* led me to check further lines of evidence bearing on the contrasting classifications and phylogenies. Two sizes of *Leptadapis*



Text-figure 26 Scatter diagram of length (l) against width (w) of upper molars of species of *Leptadapis* from various European localities: ☼ = Creechbarrow; △ = Lower Headon Beds, Hordle Cliff; ▽ = Lignite Bed, Headon Hill Limestone, Headon Hill, the smaller plot belonging to the holotype of *L. stintoni* (Gingerich); × = Lacey's Farm Quarry; + = Lower Hamstead Beds, Bouldnor Cliff; □ = Ehrenstein 1A; ◇ = holotype of *L. magnus* (Filhol) from the Quercy Phosphorites; ○ = a syntype of *L. ruetimeyeri* Stehlin (NMB Ef417) from Egerkingen α. Large rectangles span length and width measurements obtained by Gingerich (1977*b*) from Euzet. Symbols solid on left = M^1, on right = M^2 and completely solid = M^3; outline symbols = $M^{1/2}$. Data for Lacey's Farm Quarry from Insole (1972), for Ehrenstein 1A from Schmidt-Kittler (1971*b*) and for the Phosphorites from a cast. Measurements in millimetres. Lines join teeth of one individual.

appear to occur together at three further localities: 1, Ehrenstein 1A (see Text-fig. 26 and Schmidt-Kittler's (1971*b*) upper molar measurements); 2, the lignite bed in the Headon Hill Limestone (the type locality of *L. stintoni*), where a large M^3 (M20204) has been found (see Text-fig. 26); and 3, the Lower Headon Beds, where *L. magnus* occurs at Hordle Cliff and a much smaller incomplete $M^{1/2}$ from HH2 at Headon Hill. Insole (1972: 204–205, pl. 7, fig. 2) recorded as $M^{1/2}$, small enough to belong to *L. stintoni*, from the Osborne Beds of Lacey's Farm Quarry, Isle of Wight, as *A. magnus* (see Text-fig. 26). An even smaller $M^{1/2}$ has been found in the post-Grande Coupure Lower Hamstead Beds of Bouldnor Cliff (R.L.E. Ford private collection).

Acquisition of a lower molar metastylid (Text-fig. 43) appears to have stratigraphical importance (see below). Its variable occurrence in *Leptadapis* specimens from the Quercy Phosphorites housed in the BM(NH) seemed to have the potential for providing further evidence. Text-fig. 27B shows a scatter diagram of lower molars from this collection separated on



Text-figure 27 A, scatter diagram of length (l) against width (w) of lower molars of species of *Leptadapis* from various European localities: ☆ = Creechbarrow; △ = Lower Headon Beds, Hordle Cliff; ▽ = holotype of *L. stintoni* (Gingerich) from the Lignite Bed, Headon Hill Limestone, Headon Hill; □ = Ehrenstein 1A; ○ = a syntype of *L. ruetimeyeri* Stehlin (NMB Ef401) from Egerkingen α. Large rectangles span length and width measurements obtained by Gingerich (1977*b*) from Euzet. Symbols solid on left = M_1, on right = M_2 and completely solid = M_3; outline symbols = $M_{1/2}$. Data for Ehrenstein 1A from Schmidt-Kittler (1971*b*). B, Scatter diagram of length (l) against width (w) of lower molars of species of *Leptadapis* from the Quercy Phosphorites in the BM(NH): ☆ = without metastylid as in the Creechbarrow assemblage; △ = with small metastylid as in the Hordle Cliff assemblage; □ = with large metastylid as in the Headon Hill Limestone or Ehrenstein 1A assemblages; ○ = with metastylid intermediate between Creechbarrow and Hordle Cliff assemblages. Large rectangles span length and width measurements obtained by Gingerich (1977*b*) from Euzet to facilitate comparison with A. Symbols solid on left = M_1, on right = M_2 and completely solid = M_3. Measurements in millimetres. Lines join teeth of one individual.

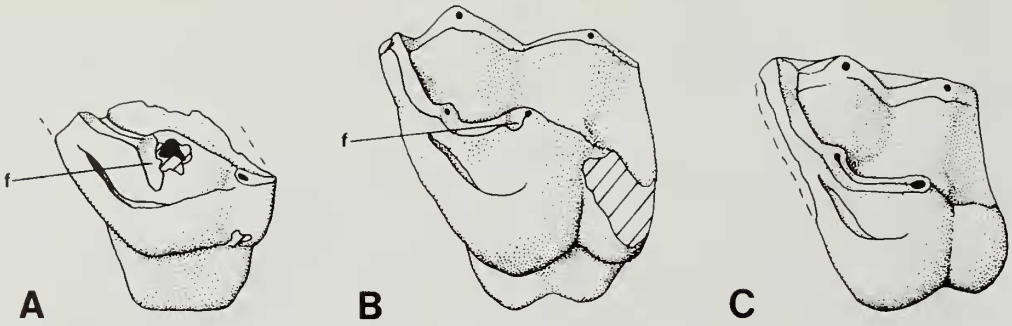
different stages in the development of the metastylid. If *L. magnus* had given rise to *L. stintoni*, one would have expected specimens with metastylid small or lacking to have been concentrated at the higher end of the size scale and those with a large metastylid at the lower end. This is not so. The plots are essentially unimodal, no specimens overlapping with *L. stintoni* (see Text-fig. 27A).

A consequence of the untenability of Gingerich's *A. magnus* → *A. parisiensis* lineage is the reinstatement of Bartonian *A. sudrei* Gingerich 1977*a* as a potential ancestor of *A. parisiensis* but not of Bartonian ?*A. laharpei* (Pictet & Humbert 1869). *A. sudrei* poses problems for the easy distinction of *Leptadapis* and *Adapis*. Various details of the cheek teeth, size of canines and first premolars, cranial and mandibular shape and structure of the humerus and astragalus (the latter two *fide* Szalay & Delson 1979: 139) facilitate separation of *A. parisiensis* from *L. magnus* and, in the case of dental characters alone, from *L. stintoni*, *L. ruetimeyeri* and *L. priscus*. According to Gingerich (1977*a*) *A. sudrei* closely resembles *Adapis parisiensis*. Nevertheless, from his measurements of mandible depth below M_1, the jaw appears to have been shallow like *Leptadapis*. *A. laharpei* was synonymized with *A. parisiensis* by Stehlin (1912: 1236–1237) but has characteristically elongated molars with widely open trigonids and an essentially central rather than slightly lingual M_{1-2} hypoconulid. Reference to either *Adapis* or *Leptadapis* is unclear. Thus the distinction of *Leptadapis* from *Adapis* is provisionally accepted herein despite the difficulty in attributing some species.

This discussion on affinities and species content is relevant for identification of the Creechbarrow material which was first listed as *Adapis* aff. *magnus* (Hooker 1977*b*). This was based on comparison with referred material of this 'well-known species'. However, the presence of two species of *Leptadapis* of slightly different sizes makes reference back to the holotype cranium of *L. magnus* important. I was unable to find mention in the literature of its repository; moreover Cray (1973: 67) stated 'specimen not located'. It was figured by Filhol (1874, 1877*b*) and Gervais (1876), but it is not clear whether or not Stehlin saw it; he briefly mentioned it, stating that it was a relatively small individual (Stehlin 1912: 1238, 1246). Dr Marc Godinot has kindly provided me with a cast of the dentition of the specimen which is in fact in the MNHN (no. Qu.11002); measurements are shown in Text-fig. 26. According to these it is not as small as Filhol's figure (1874: pl. 8, fig. 12) would suggest. It also has a shorter M^3 than specimens which have been referred to *L. magnus*, from Hordle Cliff and Euzet (Gingerich 1977*b*: fig. 1, tab. 1). It is larger than the holotype of *L. stintoni*. A further complication is that Stehlin (1912: 1277–1280, figs 286–287) named a very small and apparently primitive individual *Adapis magnus* var. *leenhardti*, which is close to *L. stintoni* in size. Unfortunately the main primitive characters noted by Stehlin (those of canine and M^3) belong to teeth missing from the holotype of *L. stintoni*.

Lower molar metastylid. Stehlin (1912: 1242) noted that the metastylid was well developed on many individuals of *L. magnus* but that it could not be considered a constant character. One specimen totally lacking this cusp he considered to be an early mutation. Its presence and size in the Hordle Cliff assemblage is fairly constant for eight specimens. There also appears to be a distinct trend for increase in development of this cusp with time as Stehlin thought, e.g. it is larger in *L. stintoni* from the Upper Headon Beds than for *L. magnus* from the Lower Headon Beds and Auversian *L. ruetimeyeri* from Egerkingen α lacks it entirely.

Large size of the lower molar metastylid is associated with a greater obliquity of the protocristid than in those individuals where the metastylid is weak or missing. By placing specimens in a morphological series, it appears that as the metastylid 'grew', the metaconid migrated distolingually, resulting in a longer, more oblique tricuspid protocristid. Concomitant changes in the upper molars should have involved distal migration of the protocone leading to a more oblique preprotocrista. This possible obliquity is difficult to observe especially in isolated teeth because of variation in angle of the mesial and buccal margins of the teeth. Details of occlusion are described by Gingerich (1972). Even though the types of *L. magnus* and *L. magnus* var. *leenhardti* do not include the lower dentition, it should be possible to judge the states of development of their metastylids, by the development (or absence) of an extra buccal phase



Text-figure 28 Oblique mesiolingual views of upper preultimate molars of *Leptadapis*, in A and B showing facet (f) on protocone caused by wear against a lower molar metastylid. A, left M^2 of holotype of *L. stintoni* (Gingerich) (M32135) from the Lignite Bed, Headon Hill Limestone, Headon Hill. B, left M^1 of *L.* aff. *magnus* (M3672) from the Lower Headon Beds, Hordle Cliff. C, right M^1 (reversed) of holotype of *L. magnus* (Filhol) (MNHN Qu11002) from the Phosphorites, Raynal (drawn from cast). All × 5·3.

facet on the upper molar protocones. This concave facet was not mentioned by Gingerich (1972), but when present is situated at the lingual end of his facet B5. Its weak development in four Hordle Cliff specimens and strong development in the holotype of *L. stintoni* matches the degree of development of their respective lower molar metastylids (see Text-fig. 28A–B). Unfortunately five further Hordle Cliff specimens in similar wear states do not show this facet; moreover, none of the Creechbarrow upper molars are well enough preserved to show presence or absence of this facet. In the holotype of *L. magnus* it is absent (Text-fig. 28C). In view of its variation in the Hordle Cliff assemblage, its absence in the holotype cannot be taken as unequivocal evidence of metastylid absence too, although it is likely that this cusp was at best fairly small in this individual. Metastylid absence in the Creechbarrow assemblage, evidence for post-Bartonian acquisition of this cusp and shortness of M^3 of Qu11002 all suggest that type *L. magnus* was probably Marinesian or early Ludian in age.

Leptadapis aff. ***magnus*** (Filhol 1874) Gervais 1876
(Pl. 11, figs 1–6; Pl. 12; Text-figs 26–28; Table 11)

v. *1977b* *Adapis* aff. *magnus* Filhol; Hooker: 141
v. *1980* *Adapis* aff. *magnus* Filhol; Hooker & Insole: 38.

HOLOTYPE OF SPECIES. Cranium (MNHN Qu11002). Phosphorites du Quercy, Raynal, France.

DIAGNOSIS OF SPECIES. No suitable diagnosis exists because of the problems discussed above. It should await comprehensive study of all available material especially from the type area.

MATERIAL. Left P^2 (M37694), right P^3 (M35441), right P^4 (M37177), left $M^{1/2}$ (M37176), right $M^{1/2}$ (M37695), left M^3 (M37696), broken right M^3 (M37178), two left lower canines (M37179–80), two right lower canines (M35442, M35754), right P_2 (M35443), three left $M_{1/2}$s (M35444, M37181–2), right $M_{1/2}$ (M35445), right M_3 (M37183), right lower molar trigonid fragment (M37184).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. P^2 is longer than broad, oblique and has a fairly broad lingual cingular shelf, lacking protocone.

P^3 is narrow lingually with poorly-developed protocone. The parastylar area is broken away. Unlike most *L. magnus* it has a metacone, which is, however, smaller than the paracone; this is recorded by Schmidt-Kittler (1971*b*: 175, text-fig. 1) for a *Leptadapis* from Ehrenstein 1A.

Table 11 Length (l) and width (w) measurements of *Leptadapis* aff. *magnus* from Creechbarrow. Measurements in millimetres.

No.	Tooth	l	w
M37694	LP^2	5·0	4·3
M35441	RP^3	(5·0)	5·8
M37177	RP^4	5·6	(6·7)
M37176	$LM^{1/2}$	6·6	7·4
M37695	$RM^{1/2}$	5·7	7·5
M37178	RM^3	5·4	–
M37696	LM^3	5·0	7·4
M37179	LC_1	–	4·3
M37180	LC_1	–	3·6
M35754	RC_1	–	4·1
M35443	RP_2	(5·0)	–
M35444	$LM_{1/2}$	7·2	5·0
M37181	$LM_{1/2}$	7·9	5·6
M37182	$LM_{1/2}$	7·0	5·0
M35445	$RM_{1/2}$	8·0	5·3
M37183	RM_3	(8·5)	(4·1)

P^4 is also typical for *L. magnus* in its length/width proportions and in having a well-developed metacone. *L. ruetimeyeri* has a much shorter P^4 (see Stehlin 1916: pl. 21, figs 27, 29–30).

The $M^{1/2}$s available are not well preserved but appear to be relatively slightly shorter than in *L. magnus*, thus rather more like those of *L. ruetimeyeri* (see Text-fig. 26; Pl. 11, fig. 4; and Stehlin 1916: pl. 21, figs 22–23, 27, 29, 31).

M^3 is also relatively short like most *L. ruetimeyeri* (see Text-fig. 26; Pl. 11, fig. 5; and Stehlin 1916: pl. 21, figs 28, 31). Stehlin (1916: pl. 21, fig. 5) showed an *L. ruetimeyeri* M^3 which is more like *L. magnus* in proportions. This tooth tends to be variable as it is the last in the row but its shortness in the Creechbarrow *Leptadapis* can be considered primitive compared with Ludian assemblages. A reduced M^3 in '*A.*' *magnus* var. *leenhardti* led Stehlin (1912: 1278) to consider this variety to be primitive and to be of Bartonian age; it is much smaller than the Creechbarrow *Leptadapis*.

M37180 (Pl. 11, fig. 6), the best preserved lower canine, is unlike the other three as well as those of *L. magnus* from various localities and that of *L. ruetimeyeri* in lacking a lingual cingulum. In two specimens from the Phosphorites du Quercy the distolingual and distobuccal crests extend separately right to the apex of the tooth, whereas on M37180 and (according to Stehlin's 1912: 1268, text-fig. 282 of NMB Ef972) *L. ruetimeyeri*, these crests die out about two-thirds of the distance towards the apex, whereupon they are replaced by a median distal crest which tops the apex. This appears to be another primitive feature of the Creechbarrow assemblage, but the character may be variable.

P_2 is broken distolingually and shows few features of interest except a high buccal cingulum.

The four $M_{1/2}$s fall into two size groups, two specimens plotting within the range of Hordle Cliff M_1s, two more plotting within the range of Hordle Cliff M_2s (Text-fig. 27A). They are tentatively distinguished likewise since their morphologies are identical. All the Creechbarrow specimens have a strong postmetacristid but no development of a metastylid in this region. The Hordle Cliff assemblage has quite a constant weak development of this cusp. Stehlin (1912: 1242) considered absence of this cusp in *L. magnus* to represent an early mutation. This idea is thus confirmed and its dating is shown to be Marinesian.

On M_3 the postmetacristid is less stongly developed than on $M_{1/2}$ but more so than on *L. ruetimeyeri* M_3. There is no entoconid.

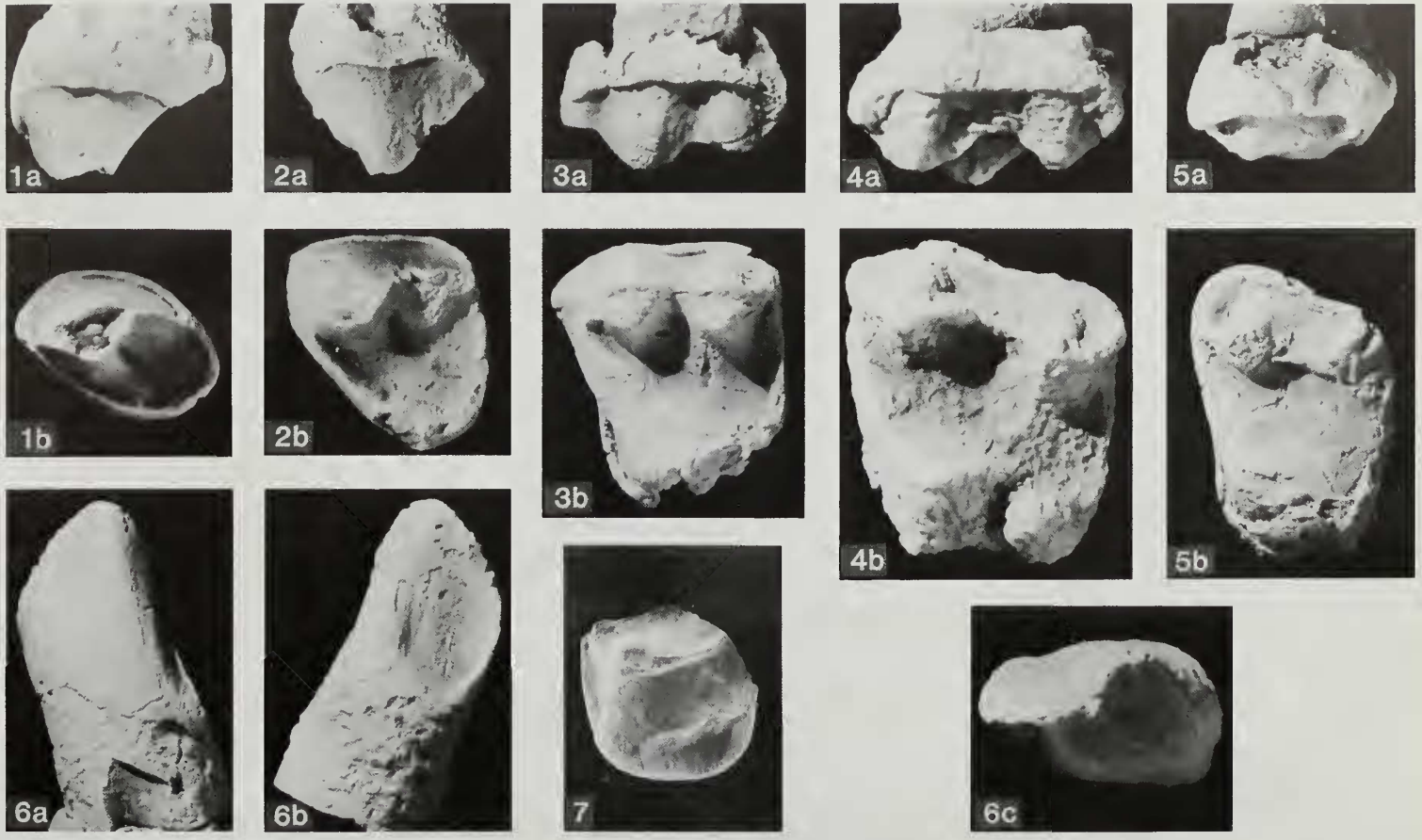


Plate 11 Teeth of Adapinae from Creechbarrow.

Figs 1–6 *Leptadapis* aff. *magnus* (Filhol). Light macrographs of upper cheek teeth and lower canine, × 6. a, buccal, b, occlusal and c, lingual views. Fig. 1a, b, left P^2 (M37694). Fig. 2a, b, right P^3 (reversed) (M35441). Fig. 3a, b, right P^4 (reversed) (M37177). Fig. 4a, b, left $M^{1/2}$ (M37176). Fig. 5a, b, left M^3 (M37696). Fig. 6a–c, left lower canine (M37180). See p. 278.

Fig. 7 Adapinae indet. Scanning electron micrograph, × 12. Lingual half of right $M^{1/2}$ (reversed) (M37692). See p. 282.

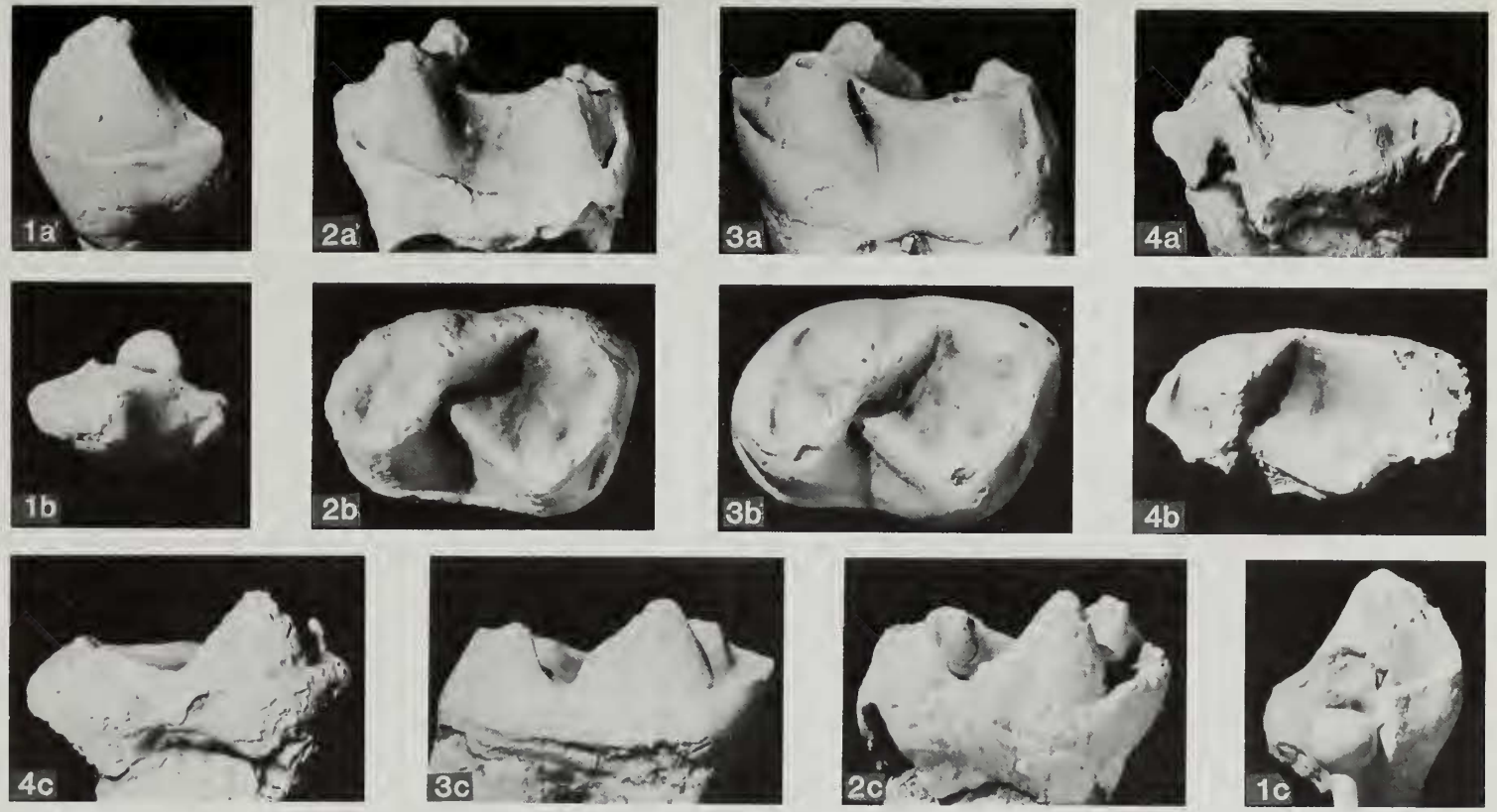


Plate 12 Light macrographs of lower cheek teeth of *Leptadapis* aff. *magnus* (Filhol) from Creechbarrow, × 6. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, right P_2 (reversed) (M35443). Fig. 2a–c, left $M_{1/2}$ (M35444). Fig. 3a–c, left $M_{1/2}$ (M37181). Fig. 4a–c, right M_3 (reversed) (M37183). See p. 278.

Thus the Creechbarrow *Leptadapis* in a variety of characters is more primitive than the referred assemblages of *L. magnus* from stratified deposits, which hitherto have all been post-Bartonian in age. In size of lower molars and width of uppers it is closer to *L. magnus* than to the small *L. stintoni* or '*L. magnus* var. *leenhardti*'. If the last should be Bartonian too, then the two lineages of *Leptadapis* must have already been established by the Marinesian. Auversian *L. ruetimeyeri* is then the best candidate for their common ancestry, giving rise to each by slight increase and decrease in size along with the relevant grade changes. The choice of name for the Creechbarrow assemblage is an attempt at conservatism, indicating probable lack of total identity with typical *L. magnus* and awaiting more material and solutions to the problems posed by the mixed faunas of the old Phosphorites collections.

Adapinae, gen. et sp. indet.
(Pl. 11, fig. 7)

Material. Lingual half of right $M^{1/2}$ (M37692).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description and discussion. This tooth fragment is indeterminate generically but is of interest as indicating the presence of a third adapine in the Creechbarrow fauna. Its length is estimated at 2·35 mm. It has a strong lingual cingulum on which is developed a small hypocone. The valley bottom between the protocone and hypocone is bridged by a very faint crest. The postprotocrista is directed distally and only slightly buccally from the protocone and only the very beginning of its bend to a buccal direction is preserved.

Its greatest similarity is with *Periconodon* but it differs in lacking a pericone completely and in the hypocone having a lesser lingual extent. These features do, however, appear to be variable in extent in the type species (cf. Stehlin 1916: pl. 22, fig. 3 with fig. 11; and see discussion by Gingerich 1977*a*: 70–71). In size it is very close. It cannot be excluded that it might be an M^2 of *Microadapis*, although here the paraconule and metaconule are prominent and the hypocone probably ought to be larger (only M^1 is known of the upper dentition of *Microadapis*).

If more material should be found supporting reference to either genus, it would mean an upward extension of stratigraphical range from the late Lutetian.

Order **RODENTIA** Bowdich 1821

Suborder **SCIUROGNATHI** Tullberg 1899

Infraorder **PROTROGOMORPHA** Zittel 1893

Family **PARAMYIDAE** Miller & Gidley 1918

One of the two named genera concerned here (*Plesiarctomys*) was placed in the Ischyromyidae, subfamily Paramyinae in Simpson's (1945) classification. Wood (1962) in a major review raised the Paramyinae to family status and the tribe Manitshini (Simpson 1941) to subfamily status, including *Plesiarctomys* in it. He also included *Ailuravus* (another genus occurring in the English Bartonian) in the Paramyidae, but *incertae sedis*. Michaux created the paramyid subfamilies Ailuravinae Michaux 1968 for *Ailuravus* and its probable ancestor *Meldimys* Michaux 1964; and Pseudoparamyinae Michaux 1964 for *Plesiarctomys* and its probable ancestor *Pseudoparamys* Michaux 1964. His two reasons for separating *Plesiarctomys* from the Manitshinae (1968: 154) were that *Plesiarctomys* represented a lineage separate from the large North American manitshines, and was derived probably from *Pseudoparamys*; and that manitshines the same age as *Pseudoparamys* were already large and thus the 'rhythm' of the *Plesiarctomys* group was different. There appears on the contrary to be little except size to prevent *Pseudoparamys* from being included also in the Manitshinae. Hartenberger (1975: 779) included the Pseudoparamyinae in the Paramyinae and considered that the grouping of *Plesiarctomys* with the North American manitshines was artificial and only founded on convergent features, but

did not give details. One cannot necessarily assume that the dental features that link the manitshines and *Plesiarctomys* are due purely to large size, since *Ailuravus*, another distinct European paramyid genus, is approximately the same size as *Plesiarctomys* but morphologically very different.

A higher taxonomic change occurred when Black (1968) showed that *Ischyromys* Leidy 1856 was scarcely more advanced in lophodonty of the cheek teeth (Wood's 1962 reason for separating it and *Titanotheriomys* Matthew 1910 in the Ischyromyidae from the Paramyidae) than are the paramyids and was closely related to them. He therefore assimilated the two families, Ischyromyidae being the prior name. He was followed by Black (1971) and Hartenberger (1975). Wood (1970) and Bosma (1974) followed Wood (1962) in placing *Plesiarctomys* in the manitshine paramyids. Wahlert (1974), in a study of the cranial foramina of protrogomorphs, concluded that *Ischyromys* was not closely related to the other genera that Black (1968) had included in the Ischyromyidae and reinstated the family Paramyidae to accommodate them. He was followed by Wood (1976*a*). Wood (1976*b*) further supported the separation of Paramyidae and Ischyromyidae on other cranial and dental evidence and (1980: 17–19) gave a full review of the dispute. Wahlert's (1974) and Wood's (1976*b*, 1980) conclusions are followed here. *Plesiarctomys* is included in the Manitshinae for strong morphological reasons and *Ailuravus* in the Ailuravinae.

Subfamily **MANITSHINAE** Simpson 1941

Genus ***PLESIARCTOMYS*** Bravard 1850

TYPE SPECIES. *P. gervaisii* Bravard 1850. Ludian, La Débruge, France.

INCLUDED SPECIES. *P. savagei* (Michaux 1968) Hartenberger 1975, *P. hartenbergeri* Wood 1970, *P. spectabilis* (Major 1873) Stehlin & Schaub 1951, *P. hurzeleri* Wood 1970 and *P. curranti* sp. nov.

RANGE. Late Ypresian to Ludian, England, France, Switzerland and ?Spain.

DIAGNOSIS (as emended by Wood, 1970). 'Medium to large sized manitshine; cresting of cheek teeth developing progressively within the genus, and more prominent than in any other manitshine except *Manitsha*; cusps of lower teeth swelling into talonid basin and reducing size of lingual gorge; P_4 small; third upper premolar progressively lost; frequently a junction of mesostyle and posterior cingulum lateral to metacone especially in P^4 and M^1; pulp cavity of incisors tending to be constricted from the sides'.

NOTE. Wood (1970) has made a thorough review of this genus and should be consulted for the early synonymies, history of investigations, comprehensive descriptions and figures of most aspects of the known species except *P. savagei*. The dental nomenclature diagram (Text-fig. 31) will suffice for most aspects of *Plesiarctomys* teeth.

Plesiarctomys curranti sp. nov.
(Pl. 13, figs 1–8; Text-figs 29, 30A)

v. *1977b Plesiarctomys* sp. 2; Hooker: 141.
v. *1980 Plesiarctomys* sp. 2; Hooker & Insole: 39.

NAME. After Mr A. P. Currant, for help with field work.

HOLOTYPE. Right M_1, M37188. Pl. 13, fig. 6.

PARATYPES. (9): Left $M^{1/2}$ (M35446), right $M^{1/2}$ (M35447), left M^3 (M37702), two right M^3s (M35448, M35763), left DP_4 (M35764), right P_4 (M35765), right M_2 (M35450), left M_3 (M35449).

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Small *Plesiarctomys*, length of M_1 = 3·3 mm. Upper and lower molars with distantly spaced buccal and lingual cusp tips, leaving broad intervening basins in which the enamel is nearly always finely wrinkled. Height of talonid basin above crown base in M_1 less than one-third of length of tooth. M_{1-2} hypolophulid absent. Lower molar sinusid broad and ectolophid complete; M^{1-2} endoloph with very shallow to absent lingual groove separating protocone from hypocone. [Mandible unknown. Incisors not definitely known].

DIFFERENTIAL DIAGNOSIS. *P. savagei* is poorly known but has an incomplete $M_{1/2}$ ectolophid.

P. spectabilis and *P. hartenbergeri* are much higher crowned; their unworn buccal and lingual cusp tips are closer together; their enamel is much more coarsely wrinkled, often in a radiating pattern; lingual groove separating M^{1-2} protocone and hypocone present.

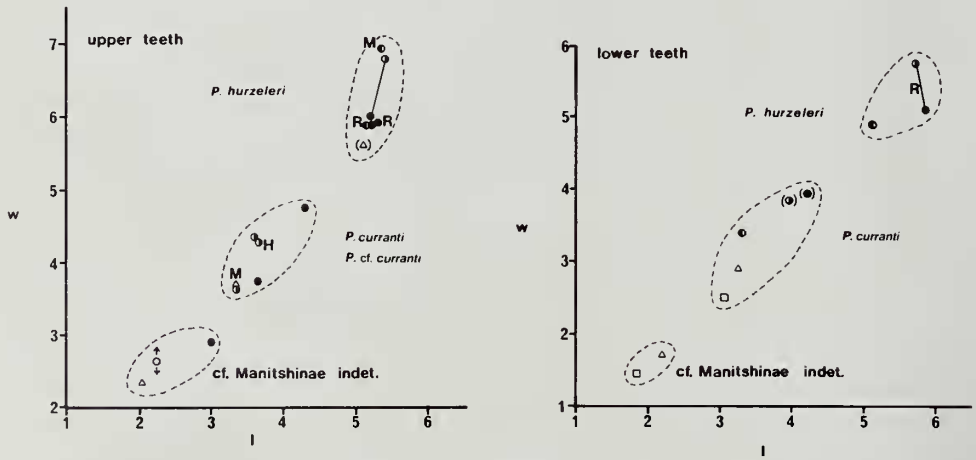
P. hurzeleri and *P. gervaisii* are larger and have partial to complete M_{1-2} hypolophulid. Enamel wrinkling replaced by a few coarse lophules in the basins. Crown height and spacing of cusps intermediate between *P. curranti* and *P. spectabilis*.

DESCRIPTION. No upper permanent or deciduous premolars have been found. The possibility of a P^4 from Mormont belonging to this species is discussed below.

$M^{1/2}$: Wood (1970: 247) distinguished between isolated M^1s and M^2s on the buccal extent of the posteroloph: i.e. in M^1 it extends buccal to the metacone, sometimes even joining the mesostyle, whereas in M^2 it stops distal to the metacone which then forms the buccal margin at this point on the tooth. On this criterion, both M35446 and M35447 are M^2s. The latter is larger than the former and its lesser proportional length is likely to be due to considerable natural wear which has removed the mesial and distal flared margins of the tooth (Pl. 13, figs 1–2).

M35446 has a prominent mesostyle but short weak mesoloph, a hypostyle is differentiated on the posteroloph and the moderate wear has only removed some of the finely granular enamel wrinkling of the trigon basin.

M35447, although considerably more worn than M35446, shows a small mesostyle detached from a somewhat longer, more prominent mesoloph; the posteroloph appears to bear no hypostyle but is joined to the metaloph by a posterolophule. Enamel wrinkling is not obvious but may have been removed by wear.



Text-figure 29 Scatter diagrams of length (l) against width (w) in upper and lower cheek teeth of *Plesiarctomys hurzeleri* Wood, *P. curranti* sp. nov., *P.* cf. *curranti* and cf. Manitshinae indet. (p. 290). □ = DP4; △ = P4; ◐ = M1; ◑ = M2; ○ = M1/2; ● = M3. Initial letters indicate that the specimens come from Mormont (M), Robiac (R) and Headon Hill 1 (H). The rest come from Creechbarrow. Measurements in millimetres.

Both teeth in mesial or distal view show a near vertical orientation of the lingual cusps relative to the plane of the crown base. This can be strongly contrasted to the very sloping orientation associated with a greater lingual crown height in *P. spectabilis* (see Text-fig. 30A–B, and Wood, 1970: 262, fig. 10A). This was referred to by Wood (1970: 246) as 'rather striking unilateral hypsodonty' and considered a generic feature, but it is less marked in *P. hurzeleri* and *P. gervaisii* and less marked still in *P. curranti*. Another feature of both M35446 and M35447 is the short buccal cingulum extending from the parastyle part way round the paracone.

M^3: Of the three M^3s only M37702 is well enough preserved to show detailed features (Pl. 13, fig. 3). M35448 is very worn and M35763 is corroded, particularly round the crown base. M37702 is large compared with the other upper molars and has rather coarse enamel wrinkling like *P. spectabilis* or *P. hartenbergeri*. The protocone has the lingual slope typical of *P. spectabilis* but lower height than in the preultimate molars of this species. M^3, however, tends to be a non-distinctive tooth, not showing the specializations often seen in $M^{1\ 2}$.

DP_4: M35764 is poorly preserved but was originally probably only slightly worn and shows the distinctive fine enamel wrinkling in the talonid basin. The complete ectolophid and high length/distal width ratio identify it as a DP_4 (Pl. 13, fig. 4). Otherwise it has few distinctive features.

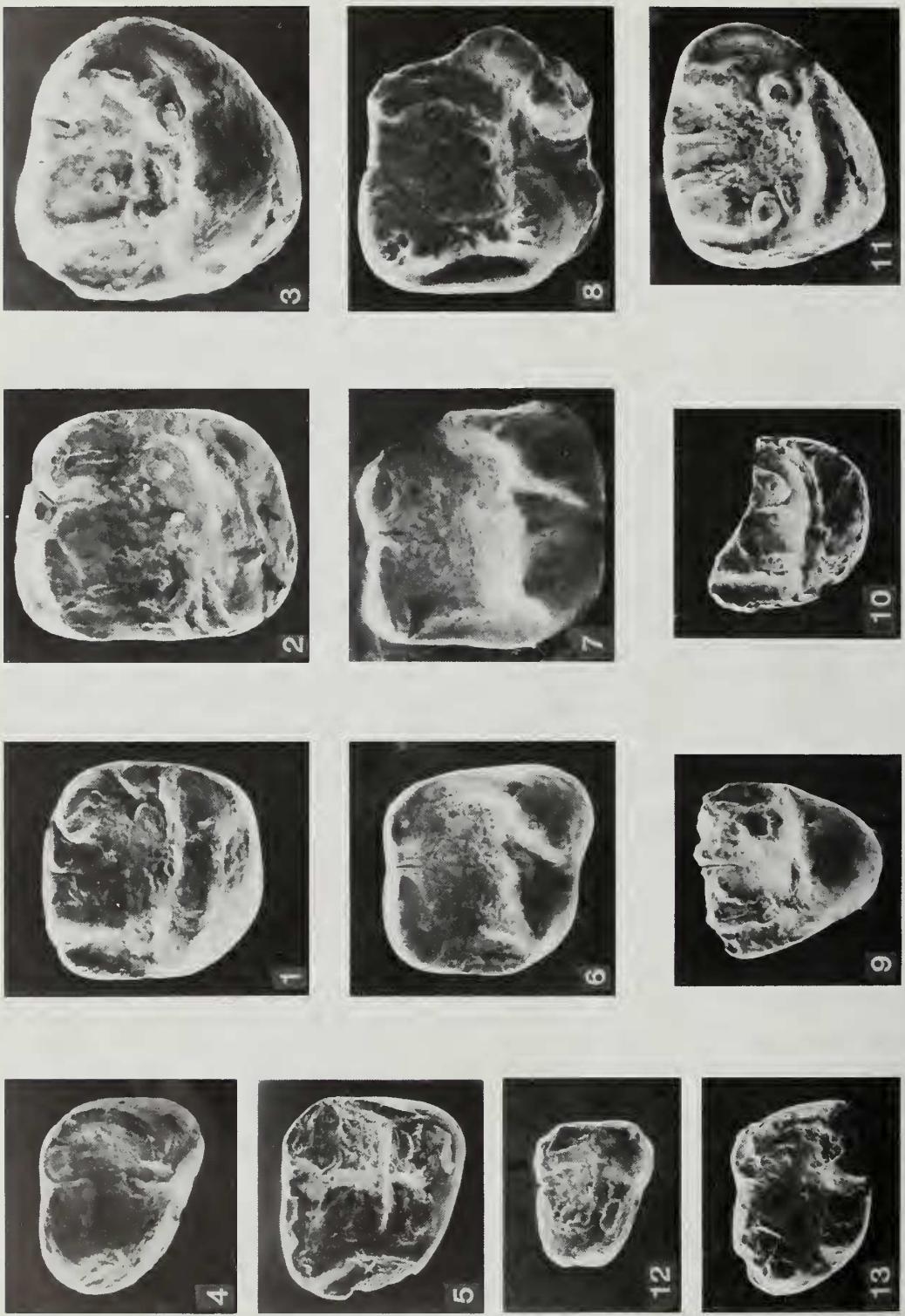
P_4: Wood (1970: 247) stated that in *Plesiarctomys* 'the trigonid is narrow ... and the protoconid usually looks merely like a basal cingulum on the metaconid. As a result the trigonid basin is minute.' M35765 has the protoconid broken away but is much broader in the region of the trigonid than in most other *Plesiarctomys* P_4s, although the protoconid is still likely to have been a small cusp (Pl. 13, fig. 5). Another peculiarity is that the sinusid is completely filled by a greatly enlarged ectostylid. There appears to have been no hypolophulid. As stated above, a high length/distal width ratio is typical of DP_4 whereas in P_4s the ratio is 1 : 1. In M35765 it is greater than 1 : 1, but the tooth can be confirmed as a P_4 because its enamel is significantly thicker than that of M35764 and the same thickness as that of the molars.

M_1: M37188 has no hypoconulid developed on the posterolophid, which is continuous but shows slight constrictions as it approaches both entoconid and hypoconid. When unworn there would probably have been interruptions. The sinusid is deep distally and there is a small but distinct mesoconid but no sign of a hypolophulid. The ectolophid is essentially complete but thin distal to the mesoconid and fissured immediately mesial to the mesoconid. The fine enamel wrinkling remains after moderate wear. The mesially tapering outline is distinctive of M_1 (Pl. 13, fig. 6).

M_2: M35450 is corroded but only slightly naturally worn (Pl. 13, fig. 7). The fine enamel wrinkling tends to be reticulate rather than granular but this may partly be due to the surface corrosion. Its outline is typically rectangular and the posterolophid, although partly broken away, appears to have been interrupted and without a hypoconulid. A small lophule extends lingually a short distance from the ectolophid but is not sufficiently distinct to deserve the term partial hypolophulid. The ectolophid is low but complete and the mesoconid is very weakly represented. The sinusid is deep distally as on M37188.

M_3: M35449 is broken at the buccal and distal edges of the crown, but is identified as M_3 because it appears to show more distal expansion than either M35450 or M37188. The tooth is hardly worn and the fine enamel wrinkling is well preserved, showing it to be partly granular, partly reticulate in pattern (Pl. 13, fig. 8). A complete hypolophulid runs from the low entoconid to the ectolophid near its distal end. It bears three small, equally spaced cuspules. The ectolophid is divided into two parts with an intervening low area, not a fissure. There is slight but not distinct formation of a mesoconid on the buccal wall of the distal half. The sinusid is deep distally. There is a deep pit towards the buccal side of the talonid basin which may be pathological.

These descriptions probably refer mainly to individual states, there being too few specimens to judge intraspecific morphological or size variation. Nevertheless, I have tried to use in the diagnosis those features shown by Wood (1970) to show the least variation in better represented species of *Plesiarctomys* and which appear to have a particular constancy within the specimens described here.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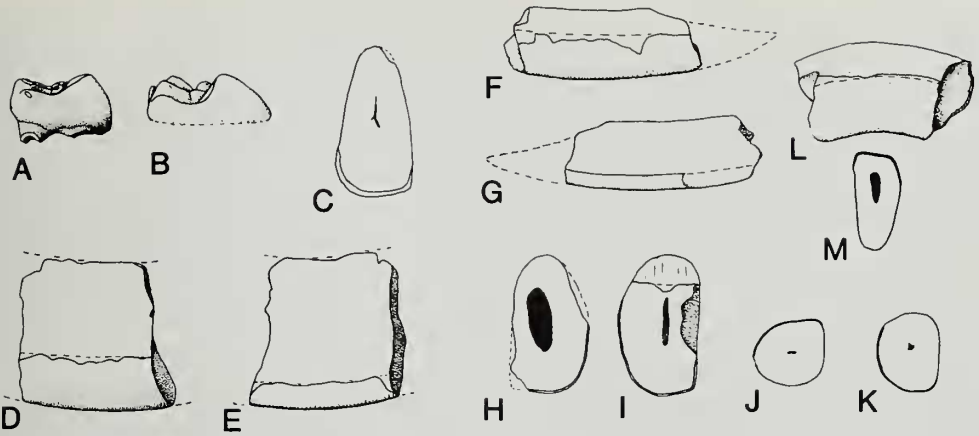

Text-figure 30 A, mesial view of left $M^{1/2}$ (M^2?) of *Plesiarctomys curranti* sp. nov. (M35446). B, mesial view of right M^2 (reversed) of *Plesiarctomys hartenbergeri* Wood (UM Bw56-17), drawn from cast. C–E, lower incisor fragment of ?*Plesiarctomys* sp. (M35451). C, transverse section; D, distal view; E, mesial view. F–I, lower right incisor of Rodentia indet. (M37190). F, distal view; G, mesial view; H, basal transverse section; I, occlusal transverse section. J–K, transverse sections of incisors of *Ailuravus stehlinschaubi* Wood. J, left upper incisor (M35698); K, right lower incisor (M37198). L–M, upper incisor fragment of Rodentia indet. (probably *Sciuroides rissonei* sp. nov. (M37391). L, distal view; M, transverse section. A–G, J–M are ×4; H–I are ×8. B is from the marnes vertes, Bouxwiller; the rest are from the Creechbarrow Limestone Formation, Creechbarrow. In the transverse sections, enamel is shown by a double line in C, H and I; and by a single thickened line in J, K and M.

One important feature is crown height, but because the cusps of *Plesiarctomys* teeth are so often worn, this is difficult to measure. It can, however, be judged by the height of the base of the talonid basin above the crown base. In *P. spectabilis* there appears to be a gradient of crown height increasing from M_3 to M_1, so that $M\frac{1}{1}$ is the best tooth in the row from which to estimate crown height differences between the species. It is partly for this reason that M_1 is chosen as the holotype of *P. curranti.*

Discussion. There are two teeth from other localities which may have affinities with *P. curranti.* The first is an M^2 from the lower part of the Lower Headon Beds of Headon Hill (HH1), Isle of Wight, described and figured by Bosma (1974: 97, pl. 4, fig. 10). It is broadly similar to the two M^2s(?) from Creechbarrow; i.e. it is similar in size and has near vertical lingual cusps which are widely spaced from the buccal cusps. It lacks, however, the short buccal cingulum on the paracone. This may not be a diagnostic character of *P. curranti* but it is not evident in any of Wood's (1970) figures of *Plesiarctomys.*

The second tooth is LGM LM 2936, a right P^4 from Mormont, Switzerland. It is distinctly more molariform than those of *P. spectabilis, P. hartenbergeri, P. savagei* or *P. hurzeleri* (P^4

Plate 13 Scanning electron micrographs of occlusal views of paramyid cheek teeth from Creechbarrow.

Figs 1–8 *Plesiarctomys curranti* sp. nov., ×10. Fig. 1, left $M^{1/2}$ (M^2?) (M35446). Fig. 2, right $M^{1/2}$ (M^2?) (reversed) (M35447). Fig. 3, left M^3 (M37702). Fig. 4, left DP_4 (M35764). Fig. 5, right P_4 (reversed) (M35765). Fig. 6, **holotype** right M_1 (reversed) (M37188). Fig. 7, right M_2 (reversed) (M35450). Fig. 8, left M_3 (M35449). See p. 283.

Figs 9–13 ?Manitshinae indet., ×12·5. Fig. 9, right P^4 (reversed) (M35452). Fig. 10, right $M^{1/2}$ (reversed) (M35767). Fig. 11, left M^3 (M35536). Fig. 12, right DP_4 (reversed) (M35768). Fig. 13, right P_4 (reversed) (M37189). See p. 290.

unknown in *P. gervaisii* but P_4 is like the other previously-described species). It also differs in being nearly as long as wide and with more widely spaced paracone and metacone; it has an incipient hypocone which is not divided from the protocone by a lingual groove on the endoloph. There is moderately fine granular enamel wrinkling. The posteroloph continues part way round the metacone buccally. The paracone and metacone are joined on the buccal edge by a ridge which is papillate but not distinctly differentiated into a mesostyle. There is a small interstitial facet, just lingual to the parastyle, indicating the former presence of P^3 or retained DP^3 (see discussion on the presence of these teeth in *Plesiarctomys* by Wood, 1970: 244–246). The suggestion that this tooth might be conspecific with *P. curranti* is based on the morphology of P_4 of this species. Its greater proportional length and consequent spacing of protoconid and hypoconid could possibly provide a pattern which could suitably occlude with the Mormont P^4. The problem can only be solved, however, by finding corresponding teeth at either Creechbarrow or Mormont. There is no information on the label with the Lausanne Museum specimen as to whether it came from Eclépens-Gare or Entreroches.

Two lower incisor fragments from Creechbarrow (M35451, M35766) too large to belong to any of the pseudosciurids known by their cheek teeth at this locality are potential candidates for attribution to the present species. The more complete (M35451) is slightly narrower than the species with the narrowest lower incisors (*P. hartenbergeri*) (Text-fig. 30C–E). In fact the proportions are more that of a pseudosciurid. If the incisor should really belong to *P. curranti*, its length/width proportions would be a further diagnostic character. In the broken section of the dentine, it is just possible to see a triangular, laterally pinched pulp cavity typical of *Plesiarctomys*.

Plesiarctomys hurzeleri Wood 1970
(Pl. 14, figs 1–3; Text-fig. 29)

vp. 1873 *Sciuroides* sp.; Major: pl. 3, fig. 7.
v* 1970 *Plesiarctomys hurzeleri* Wood: 255–257, figs 5–6.
v. *1977b* *Plesiarctomys* sp. 1; Hooker: 141.
v. *1980* *Plesiarctomys* sp. 1; Hooker & Insole: 39.

HOLOTYPE. Left mandibular ramus with M_{1-2} (FSL 4912). Lower Calcaire de Fons, Robiac, Gard, France.

RANGE. Marinesian, Creechbarrow, England; Robiac and La Millette, France (Wood's 1970 discrediting of the last record arose from his confusion between Castres and Castrais, localities of different ages). Also from the fissure deposits of Mormont, Switzerland, and Quercy, France.

MATERIAL. Left P^4 (M35761); right M^{2-3} (M37185); left M^3 (M37186) (possibly the same individual as M37185); left M_1 (M37187); and a fragment of left $M_{1/2}$ (M35762).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

EMENDED DIAGNOSIS. Medium-sized *Plesiarctomys*, length of M_2 = 5·38 mm. Upper and lower molars with moderately spaced buccal and lingual cusp tips, with shallow intervening basins with a few coarse lophules and no enamel wrinkling. Height of talonid basin above crown base in M_1 about half the length of the tooth. M_{1-2} hypolophulid nearly continuous. Lower molar sinusid narrow and ectolophid complete. M^{1-2} endoloph with very shallow to absent lingual groove separating protocone from hypocone. Anterior margin of pterygoid fossa of mandible vertical. Upper incisors nearly as long (mesiodistally) as wide (buccolingually), with one or two faint sulci.

REASONS FOR EMENDATIONS. Characters here removed from Wood's (1970) diagnosis are those which I consider are subject to individual variation and had originally been included because no more than one specimen of any cheek tooth type was then known.

1. The apparent absence of two hypoconulids from the Creechbarrow M_1 and the variation of this character in *P. gervaisii* (Wood 1970: 253, figs 4A–C) make it unsuitable as a specific character.

2. The presence of only three roots (one mesial, two distal) instead of four in the Creechbarrow M_1 and some variation in their number in *P. spectabilis* (Wood 1970: 265) requires emendation of this character. For *P. gervaisii*, Wood (1970: 249) stated 'lower molars with three or, rarely, four roots apiece', but (1970: 254) 'All of the lower molars preserved have three roots'. In view of the other close similarities of the Creechbarrow M_1 to the holotype of *P. hurzeleri*, it seems best to consider these as conspecific and the root number as slightly variable.

3. Variation in size of M^1 hypocone in *P. gervaisii* (Wood 1970: 251, figs 2A, C, D) suggests that a similar degree of difference between the Creechbarrow and Robiac upper preultimate molars is not of specific value.

4. Other modifications are to make the diagnosis compare feature for feature with *P. curranti*.

DIFFERENTIAL DIAGNOSIS. *P. savagei* is smaller and has an incomplete $M_{1/2}$ ectolophid.

P. spectabilis and *P. hartenbergeri* are smaller and higher-crowned; their unworn buccal and lingual cusp tips are closer together; their enamel is coarsely wrinkled, often in a radiating pattern; a lingual groove separating M^{1-2} protocone and hypocone is present; they have one mesial and one distal lower molar root; their incisors lack sulci; and *P. hartenbergeri* incisors are also relatively shorter.

P. gervaisii is slightly larger and has two mesial and one distal lower molar roots.

P. curranti is smaller and lower-crowned; its unworn buccal and lingual cusp tips are further apart; its enamel is finely wrinkled; its lower molar sinusid is broader.

DESCRIPTION. P^4: This tooth is badly corroded but is important as being the first upper premolar to be attributed to this species (Pl. 14, fig. 1). This is based on size and the steeper slope of the lingual wall compared to *P. spectabilis*. From Wood's (1970) figures, the outline of *P. spectabilis* P^4 varies considerably and M35761 does not differ significantly except that the parastyle is more prominent, thus increasing the length/width ratio. A small hypocone is weakly differentiated from the protocone on the postprotocingulum. The paraconule is buccal to the midline and the paracone and metacone appear small and joined by a strong buccal cingulum with no sign of a mesostyle or mesoloph. However, bad preservation makes clear recognition of cusps and crests difficult. The tooth is less square and less molarized than LM 2936 from Mormont described under *P. curranti* (p. 287).

M^2: Almost square in outline (Pl. 14, fig. 2) in contrast to the triangular right $M^{1/2}$ (FSL 4916) from Robiac (Wood 1970: 256, fig. 6A), but very similar to the right $M^{1/2}$ from Mormont (LGM 40463: LM 2935) (figured by Major, 1873: pl. 3, fig. 7 as *Sciuroides* sp.). In both the Creechbarrow and Mormont specimens, the hypocone is larger than in FSL 4916 and there is a strong mesoloph stemming from a weak mesostyle. Unfortunately both teeth are considerably worn, obscuring most of the detail.

M^3: The suggestion that M37185 and M37186 belong to the same individual is based on near identity of wear and morphology of the M^3s and matching interstitial facets of right M^2 and M^3, supported by similar wear and preservation (Pl. 14, fig. 2). All three teeth came from the same excavation hole. The outline of the two M^3s from Creechbarrow tapers more rapidly than in the right M^3 (FSL 4917) from Robiac, which is trapezoidal, having a lingually more salient hypocone. There is some evidence of a mesoloph, lacking on FSL 4917. That specimen has a gap between the mesostyle and metacone, whereas the Creechbarrow M^3s have a continuous buccal cingulum. Other potential features have been removed by wear.

M_1: M37187 is identified as an M_1 rather than an M_2 because the outline has a slight mesial taper (Pl. 14, fig. 3). It otherwise differs from the M_2 of the holotype (Wood 1970: 255, fig. 5A) in having a wider sinusid; no obvious differentiation of the posterolophid into two hypoconulids; the hypolophulid joining the mesoconid instead of the hypoconid; a stronger ectolophid; and a single mesial root pinched in the middle. More specimens of lower molars are required before the exact degree of variation in root number can be assessed.

The left $M_{1/2}$ (M35762) is broken and corroded but shows a strong ectolophid and the hypolophulid joining the mesoconid as in M37187.

Discussion. *P. hurzeleri* appears to be very closely related to *P. gervaisii* from which it differs mainly in slightly smaller size. It could stand as a good morphological ancestor for *P. gervaisii*, whose type horizon is higher (late Ludian). That *P. gervaisii* may have already evolved by the earliest Ludian is suggested by the presence at Eclépens of a P_4 (NMB Mt.1468), mentioned by Wood (1970). This locality contains fissures of both Marinesian (Eclépens-Gare and Eclépens A) and earliest Ludian (Eclépens B) age (see correlation section, pp. 422–429). The *P. hurzeleri* $M^{1/2}$ (LGM 40463: LM 2935) from Mormont unfortunately lacks more detailed locality data.

?**Manitshinae**, gen. et sp. indet.
(Pl. 13, figs 9–13; Text-fig. 29)

v. *1980 Plesiarctomys* sp. 3; Hooker & Insole: 39.

Material. Right P^4 (M35452); broken right $M^{1/2}$ (M35767); left M^3 (M35536); right DP_4 (M35768); right P_4 (M37189).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. The specific association of these teeth is by no means certain. They are smaller than any known species of *Plesiarctomys* except perhaps the unnamed upper premolar from the Lutetian of Montllobar, Spain, described by Wood (1970: 271). Apart from size, the upper teeth share prominent isolated or near isolated paraconules and metaconules and the lack of the typically inflated robust appearance of *Plesiarctomys* teeth. Their morphology is approached only slightly by the low-crowned, basined teeth of *Plesiarctomys curranti*. The anteroloph, endoloph and posteroloph form a single three quarters encircling loph on which protocone and hypocone can hardly be individually recognized.

P^4: This tooth lacks the buccal wall and is triangular in outline (Pl. 13, fig. 9). Large paraconule and metaconule arise from narrow preprotocrista and postprotocrista respectively. The metaconule is more isolated than the paraconule. The anteroloph broadens buccally towards a parastyle which is mainly broken away. A fissure separates paracone and metacone. The posteroloph bulges slightly distolingually but there is no sign of a hypocone.

$M^{1/2}$: A large buccal part of this tooth is missing (Pl. 13, fig. 10). It is considered to be a right because the more isolated of the two intermediate conules by comparison with P^4 appears to be the metaconule; and also because the more prominent of the two lingual cusps is probably the protocone.

M^3: This well-preserved tooth, unlike the previous two, is scarcely worn (Pl. 13, fig. 11). Its outline is a right-angled triangle with the distolingual edge as the hypotenuse and the mesial edge the shortest side. The metacone is only slightly smaller than the paracone and the metaconule is larger than the paraconule. There is no hypocone and the prominent posteroloph bulges distally and meets the metacone buccally. There is a prominent mesostyle terminating a strong mesoloph which extends one third the distance across the trigon basin. Distal to the main mesostyle is a fissure and then a small accessory mesostyle joined to the metacone. The enamel is finely wrinkled and two slightly coarser folds occur buccal and lingual of the paraconule. Protocristae are lacking except for a slight development between the metaconule and protocone; and the paraconule and metaconule would have remained distinct even after heavy wear. The anteroloph is weak and forms only a narrow shelf in front of the paracone.

DP_4: This tooth is corroded and enamel is missing from its buccal wall, but it shows finely wrinkled enamel in the talonid basin (Pl. 13, fig. 12). It is identified as a DP_4 by analogy with the high length/width ratio of this tooth compared to P_4 in *Plesiarctomys*. There appears to be a nearly complete hypolophulid joining the hypoconid as can occur in *Plesiarctomys* (see Wood 1970: fig. 12K). The large mesial cusp probably combines both protoconid and metaconid and there is no cingulum mesial to this.

P_4: This tooth is also corroded and distobuccally broken (Pl. 13, fig. 13). It has a distinct protoconid which is slightly smaller than the metaconid, as in *Plesiarctomys curranti*. There is a deep talonid notch, no hypolophulid and the talonid basin enamel is finely wrinkled.

DISCUSSION. This small assemblage probably belongs to an undescribed genus. Despite some similarities, it does not fit the diagnosis of *Plesiarctomys*. There are some striking similarities to the 'genre indéterminé B' from the early Eocene of Avenay and Condé-en-Brie, France, of Michaux (1968: pl. 10, figs 7–9). The large isolated intermediate conules, strong encircling lingual loph with indistinct cusps, and finely wrinkled, deeply basined trigon are features in common, suggesting that the two taxa may be congeneric. That they are distinct at species level is indicated by the absence of a hypocone on the Avenay upper preultimate molar.

Michaux (1968) did not place his 'genre indéterminé B' in any paramyid subfamily. The suggestion that the present form might be a manitshine is based on its vague similarity to *Plesiarctomys*.

A rodent lower right incisor from Creechbarrow (M37190) (Text-fig. 30F–I) fits none of the other taxa described here, unless it is a juvenile *Ailuravus*. It is the correct size for the present form, and has some unusual features. It is an almost symmetrically compressed D-shape in cross section and has a buccolingually elongated pulp cavity, not triangular or dagger-shaped as in *Plesiarctomys*. There is a single distobuccal carina. The enamel is as thin as in the incisors of *Ailuravus*. The mesial enamel band extends one fifth of the width (buccolingual) of the tooth. Distally the enamel extends more than half way round the tooth. From figures in Wood (1962) this degree of enamel extension occurs in *Ischyrotomus compressidens* (Peterson 1919), *Reithroparamys debequensis* Wood 1962, *Leptotomus sciuroides* (Scott & Osborn 1890), *L. mytonensis* Wood 1962, *L. bridgerensis* Wood 1962, *L. parvus* Wood 1959, *L. huerfanensis* Wood 1962, *L. costilloi* Wood 1962, *L. grandis* Wood 1962, *L. leptodus* (Cope 1883), *Paramys delicatior* Leidy 1873 and *P. delicatus* Leidy 1873 amongst the North American paramyids and *Ailuravus* spp. amongst the European ones. It does not occur, however, in *Paramys francesi*, the species that Michaux (1968: 175) considered closest to his 'genre indéterminé B'. This could be a primitive character of no importance in isolation, or M37190 may not belong to the same species as the other teeth assigned to the present form.

Subfamily **AILURAVINAE** Michaux 1968

DIAGNOSIS. See Wood, 1976*a*: 122.

Genus ***AILURAVUS*** Rütimeyer 1891

[incl. *Palaeomarmota* Haupt 1921, *Megachiromyoides* Weigelt 1933, *Aeluravus* and *Maurimontia* Stehlin & Schaub 1951]

TYPE SPECIES. *Ailuravus picteti* Rütimeyer 1891. Late Lutetian fissure fillings, Egerkingen, Canton Solothurn, Switzerland.

INCLUDED SPECIES. *A. michauxi* Hartenberger 1975, *A. macrurus* Weitzel 1949, *A. stehlinschaubi* Wood 1976*a*.

RANGE. Late Ypresian to Bartonian; Britain, France, East and West Germany and Switzerland.

EMENDED DIAGNOSIS. See Wood, 1976*a*: 123–124.

REMARKS. Following Wood (1976*a*: 145) it is considered that the two species described but not named by Michaux (1968: 159–161) fall within the variation of a single species. They were later named by Hartenberger (1975: 780–781) but his diagnoses do not allow them to be distinguished and no measurements were given. Therefore, *A. remensis* Hartenberger 1975 (p. 781) is herein synonymized with *A. michauxi* Hartenberger 1975 (p. 780) on page priority.

The four species listed above are not easy to distinguish because of the small number of specimens of each species and the large amount of individual variation. Even though *A. macrurus* is known from complete skeletons with fur preserved, the teeth are usually in occlusion and cannot easily be seen. Creechbarrow is only the second known locality for *A. stehlinschaubi* and considerably increases the number of teeth known. DP^3, P^3, DP_4, I^1 and I_1 were previously unknown.

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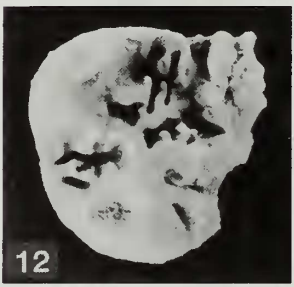
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Ailuravus stehlinschaubi Wood 1976*a*
(Pl. 14, figs 4–13; Text-fig. 30J–K; Table 12)

v. 1869 *Hyracotherium* Owen?; ?Pictet & Humbert: pl. 25, fig. 5.
v. 1951 *Maurimontia picteti* Stehlin & Schaub: 20, fig. 18; 206, fig. 310.
v. 1962 *Maurimontia picteti* Stehlin & Schaub; Wood: 239, fig. 88G–H.
v* 1976*a* *Ailuravus stehlinschaubi* Wood: 141–145, fig. 6.
v. *1977b* *Ailuravus stehlinschaubi* Wood; Hooker: 141–142.
v. *1980* *Ailuravus stehlinschaubi* Wood; Hooker & Insole: 39.

HOLOTYPE. Right maxilla with DP^4, P^4–M^3 (LGM 39559: LM 2906). Bartonian fissure filling, Eclépens-Gare, Canton Vaud, Switzerland.

PARATYPES. Right mandibular ramus with chipped P_4–M_3 (LGM 39561: LM 2910), and left M^1 (NMB Mt1767). Occurrence as holotype.

MATERIAL. DP^3 (M35453); P^3 (M35769); DP^4 (M35771); 3 P^4s (M35770, M37191–2); 6 $M^{1/2}$s (M35454–6, M35772, M37193, M37697); 2 DP_4s (M35774–5); $M_{1/2}$ (M35457); 8 trigonid and talonid fragments of $P_4/M_{1/2}$ (M35458–9, M35776–8, M35780, M37194, M37698); M_3 trigonid (M35779) and talonid (M35773) fragments; 12 undetermined fragments of cheek teeth (M35460–3, M35784, M37195); I^1 (M35698); and 6 I_1s (M35781–3, M37196–8).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

RANGE. Recorded only from the Bartonian of Eclépens-Gare, Switzerland; and Creechbarrow, England.

EMENDED DIAGNOSIS. (Slightly modified from Wood, 1976*a*: 142). Large species of *Ailuravus*, length of $M^1 = 4{\cdot}50$–$5{\cdot}14$ mm (see also measurements in Table 12 and Wood, 1976*a*: 127); cusps (especially conules) of upper cheek teeth tend to be elongate mesiodistally; valleys between cusps deep; enamel wrinkling moderate to dense; single paraconule; metaconule developing a mesio-distal elongation or doubling; protostyle weak to missing; mesostyle very prominent and buccally extended, especially on P^4; M^{1-2} with hypocone consistently only slightly smaller than protocone; M^3 without hypocone; mesoconid of lower teeth very large, triangular, and cut off from buccal margin of tooth; posterolophid of molars almost non-existent except for the hypertrophied hypoconulid; incisors almost circular in cross section and small (I_1 mesiodistal dimension 40–52% of $M^{1/2}$ length); mental foramen more than the length of P_4 in front of P_4.

DIFFERENTIAL DIAGNOSIS. *A. michauxi* is smaller with cone-shaped intermediate conules on upper cheek teeth; valleys shallow with much less enamel wrinkling; paraconule may be double; protostyle prominent; mesostyle and hypocone smaller; molar posterolophid more continuous; [incisors and jaw unknown].

A. macrurus has cone-shaped intermediate conules; valleys shallow with much less enamel wrinkling; paraconule double; protostyle prominent; mesostyle smaller; hypocone may be smaller; molar posterolophid more continuous; incisors more buccally tapered and slightly larger; mental foramen more posterior.

A. picteti has less elongate intermediate conules; valleys may be shallower and may have less enamel wrinkling; paraconule double; protostyle may be prominent; mesostyle smaller; hypo-

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Plate 14 Light macrographs of occlusal views of cheek teeth of paramyids from Creechbarrow, × 8.
Figs 1–3 *Plesiarctomys hurzeleri* Wood. Fig. 1, left P^4 (M35761). Fig. 2, right M^{2-3} (reversed) (M37185). Fig. 3, left M_1 (M37187). See p. 288.
Figs 4–13 *Ailuravus stehlinschaubi* Wood. Fig. 4, right DP^3 (reversed) (M35453). Fig. 5, left DP^4 (M35771). Fig. 6, left P^3 (M35769). Fig. 7, left P^4 (M37191). Fig. 8, right $M^{1/2}$ (reversed) (M37193). Fig. 9, left DP_4 (M35775). Fig. 10, left P_4? trigonid fragment (M35778). Fig. 11, right $M_{1/2}$ (reversed) (M35457). Fig. 12, left M_3 trigonid fragment (M35779). Fig. 13, left M_3 talonid fragment (M35773). See above.

Table 12 Length (l) and mesial (w_1) and distal (w_2) width measurements of *Ailuravus stehlinschaubi* from Creechbarrow. Only one width measurement is given for incisors and upper cheek teeth. Measurements in millimetres.

No.	Tooth	l	w_1	w_2
M35453	DP^3	2·30	1·85	
M35769	P^3	2·70	2·35	
M35770	P^4	(5·20)	–	
M37191	P^4	(5·70)	6·30	
M37192	P^4	5·35	–	
M35454	M^1?	4·50	–	
M35772	M^1?	4·75	5·55	
M37193	M^1?	4·95	5·60	
M37697	M^2?	4·75	5·25	
M35774	DP_4	(4·50)	3·10	(3·60)
M35775	DP_4	4·20	(2·60)	(3·25)
M35778	P_4?	–	3·45	–
M35780	P_4?	–	3·45	–
M37698	P_4?	–	–	3·75
M35457	$M_{1/2}$	4·90	3·80	4·35
M35458	$M_{1/2}$	–	3·45	–
M37194	$M_{1/2}$	–	3·65	–
M35459	$M_{1/2}$	–	–	4·30
M35776	$M_{1/2}$	–	–	4·15
M35779	M_3	–	4·00	–
M35773	M_3	–	–	3·55
M35698	I^1	2·60	2·40	
M35781	I_1	2·05	2·60	
M35782	I_1	2·15	(2·90)	
M35783	I_1	2·05	(2·90)	
M37196	I_1	2·00	2·35	
M37197	I_1	2·30	2·85	
M37198	I_1	2·35	2·95	

cone may be smaller; mesoconid usually joined to hypoconid by buccal spur as well as by ectolophid; incisors slightly larger (inferred from alveoli); mental foramen more posterior.

DESCRIPTION. Wood (1976*a*) has described this species in detail, so only new features or variations will be dealt with here. Most of the tooth measurements of the Creechbarrow material are slightly less than their counterparts in the type series (see Table 12 and Wood, 1976*a*: 126–127, tabs 1–2).

Wrinkling of the enamel is very variable in extent and detail. It may be relatively weak (Pl. 14, fig. 7) or very strong (Pl. 14, fig. 8). It usually has a narrow core of dentine. Because of the variation, there is overlap with *A. picteti*, but here the degree of wrinkling is usually less.

DP^3 and P^3 (Pl. 14, figs 4, 6): Wood (1976*a*: 143–144) suggested that these teeth were probably absent in the holotype, referring to the absence of alveoli in Stehlin & Schaub's (1951) fig. 18, drawn before jaw breakage caused by DP^4 removal. However, Pictet & Humbert's (1869: pl. 25, fig. 5b) buccal view shows the maxilla to have been truncated immediately anterior to DP^4. The question can never be settled for the holotype, but M35453 and M35769 show the morphologies of DP^3 and P^3 respectively and indicate that both these teeth could occur in *A. stehlinschaubi*. M35453 is the smaller and has much thinner enamel than M35769 or any of the P^4s or molars, which is typical for a milk tooth. It has a prominent parastyle, distally placed ?paracone with two distal crests, a minute ?protocone at the distolingual corner and a ?preparacrista with a small cuspule at about its midpoint. M35769 is narrower distally, has a central paracone with a buccally flexed postparacrista which joins a distal cingulum bearing a

small lingual cuspule; a curved crest runs down the lingual side of the paracone; there is neither parastyle nor protocone.

DP^4 (Pl. 14, fig. 5): This tooth is broken mesiobuccally but is essentially similar to that of the holotype DP^4.

P^4: M37191 is lacking most of the parastyle but from the spacing of its main cusps seems to be relatively broader than the holotype P^4, has slightly more wrinkled enamel and a small hypocone (Pl. 14, fig. 7). M35770 has the protocone broken away and is much more densely wrinkled than either M37191 or the holotype. M37192 is heavily, naturally worn and shows a similar degree of wrinkling to M37191.

$M^{1/2}$: M^1 and M^2 of the holotype can be distinguished on length/width ratio. Among the isolated Creechbarrow upper preultimate molars, the shorter broader ones are tentatively identified as M^1 and the single relatively longer one as M^2. There is high variation in enamel wrinkling, buccal cingulum strength and mesostyle size. There are also differences in the distal elongation or doubling of the metaconule: in M35772 and M37697 there is a second metaconule developed distal to the first; in M35454 and M35455, the first metaconule has a strong distal crest extending to the distal cingulum; and in M37193, the whole area distal to the first metaconule is covered with dense enamel wrinkling (Pl. 14, fig. 8).

DP_4 (Pl. 14, fig. 9): Two submolariform teeth (M35774 and M35775) have thinner enamel than any of the molars and so are identified as DP_4, a tooth not previously recorded for the genus *Ailuravus*. They show variation in degree of enamel wrinkling, as do the molars. The principal differences from the holotype P_4 are presence of a smaller, rounder, less triangular mesoconid, large isolated lingually situated hypoconulid, an extensive cingulum-bordered sinusid and lower crown height.

Lower Permanent Cheek Teeth: Only the $M_{1/2}$, M35475, is complete (Pl. 14, fig. 11). All the others are either trigonid or talonid fragments. The M_3 talonid (M35773) shows, better than the poorly preserved paratype, the crescentically crested hypoconid and the almost total isolation of this cusp, the hypoconulid, entoconid and mesoconid (Pl. 14, fig. 13). The trigonid (M35779) is identified as M_3 because of the distal position of the protoconid relative to the metaconid and the apparent depth of the ectoflexid (Pl. 14, fig. 12). The remaining talonid fragments add little to our existing knowledge of the species. Of the trigonids, those with the more convergent cusps are tentatively identified as P_4 (e.g. Pl. 14, fig. 10) from comparison with the admittedly imperfect paratype premolar and molars.

Incisors: The finding of seven *Ailuravus* incisors at Creechbarrow is in marked contrast to the normal rarity of these teeth (see Wood, 1976*a*: 125). The cross-sectional shape of the lowers is similar to that of *A. macrurus* figured by Wood (1976*a*: fig. 5G), but rounder (Text-fig. 30K). The single upper is also much rounder than Wood's (1976*a*: fig. 5D) figured I^1 of *A. macrurus* (see Text-fig. 30J).

Discussion. Although not recorded from other localities, it is possible that the record of Ailuravinae gen. indet., which is an incisor (J.-L. Hartenberger, personal communication 1978), from Robiac (Sudre 1969*a*: tab. opposite p. 142) might be shown to belong to this species if cheek teeth can be found.

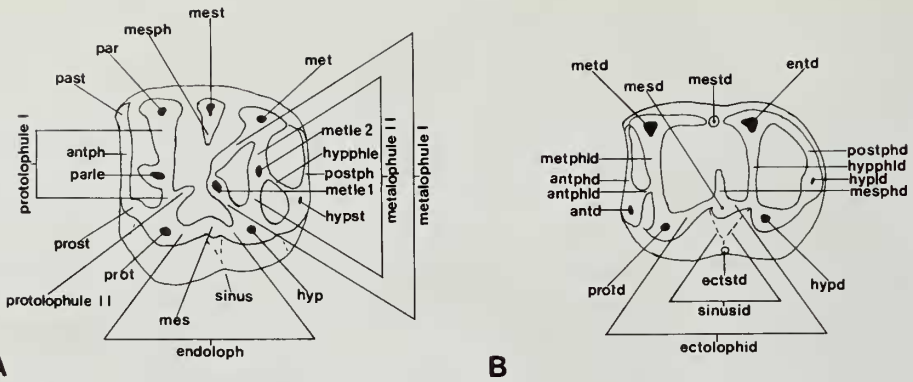
Wood (1976*a*: 145) considered *A. stehlinschaubi* to have descended from Lutetian *A. picteti*. The *Ailuravus* sp. indet. from the Auversian Sables à *Batillaria bouei* (Sables d'Auvers) of Arcis-le-Ponsart, Marne, France, may provide an intermediate between the two (Louis 1976: 49).

Thus *A. stehlinschaubi* is a good age marker for the European Bartonian, if not more strictly the Marinesian. The genus appears to have become extinct at the end of the Bartonian.

Infraorder uncertain

Superfamily **THERIDOMYOIDEA** Alston 1876

This superfamily has been classifed in various ways infraordinally in the Rodentia (e.g. Schaub 1958, Romer 1966, Simpson 1945), but it is probably derived from subfamily Paramyinae of the



Text-figure 31 Dental nomenclature of pseudosciurid cheek teeth. A, left upper molar. Buccal edge towards top of page, lingual towards bottom. B, left lower molar. Buccal edge towards bottom of page, lingual towards top.

Abbreviations:

A. antph—anteroloph
hyp—hypocone
hypphle—hypolophule
hypst—hypostyle
mes—mesocone
mesph—mesoloph (partial)
mest—mesostyle
met—metacone
metle 1—metaconule 1
metle 2—metaconule 2
par—paracone
parle—paraconule
past—parastyle
postph—posteroloph
prost—protostyle (= anterocone)
prot—protocone

B. antd—anteroconid
antphd—anterolophid
antphld—anterolophulid
ectstd—ectostylid
entd—entoconid
hypd—hypoconid
hypld—hypoconulid
hypphld—hypolophulid
mesd—mesoconid
mesphd—mesolophid (partial)
mestd—mesostylid
metd—metaconid
metphld—metalophulid
postphd—posterolophid
protd—protoconid

Paramyidae (see Hartenberger 1969: 56). No evidence is forthcoming on these questions from the English Bartonian material. Suffice to say that theridomyoids are hystricomorphous and sciurognathous and have cheek teeth which range from low-crowned to moderately high-crowned but always retain the roots. The complexities of convergence in hystricomorphy are discussed by Wood & Patterson (1970). Their dental formula is $\frac{1\ 0\ 1\ 3}{1\ 0\ 1\ 3}$ but sometimes $DP\frac{4}{4}$ is retained and not replaced by $P\frac{4}{4}$.

They have usually been divided into two families: the Pseudosciuridae Zittel 1893 for the lower-crowned and Theridomyidae Alston 1876 for the higher-crowned types. However, Hartenberger (1971) produced a model of parallel evolution of higher-crowned forms (which would have been classified as theridomyids) from new (*Estellomys*) and hypothetical lower-crowned forms (which would have been classified as pseudosciurids or as transitions between the two families). He assimilated the two families under the name Theridomyidae which he divided into six subfamilies, all considered to be monophyletic. These were later increased to seven (Hartenberger 1973) and comprised: Pseudosciurinae Zittel 1893, Oltinomyinae Hartenberger 1971, Sciuroidinae Hartenberger 1971, Columbomyinae Thaler 1966, Theridomyinae Alston 1876, Issiodoromyinae Lavocat 1951 and Remyinae Hartenberger 1973, with the genus *Quercimys* Thaler 1966 of uncertain family status. *Tarnomys* was described later (Hartenberger & Schmidt-Kittler 1976), but although considered related to *Pseudosciurus*, it was classified at no lower level than superfamily Theridomyoidea. The Pseudosciurinae and Sciuroidinae contained all the genera which had been included in the Pseudosciuridae before 1973. Bosma (1974) accepted the traditional separation of the Pseudosciuridae and Theridomyidae and considered that Hartenberger's transition forms should be placed arbitrarily in one or the other family. She

did not recognize the subfamily division of the Pseudosciuridae (presumably meaning the Pseudosciurinae and Sciuroidinae) but gave no further explanation.

This division into two subfamilies is untenable for the following reasons. Hartenberger (1973) described a new species of *Suevosciurus* (*S. romani*) in the Pseudosciurinae which in fact is identical with *Sciuroides siderolithicus*, type species of the type genus of the Sciuroidinae. Therefore the type species of *Sciuroides* was included in both the Pseudosciurinae and Sciuroidinae. Apart from *S. siderolithicus*, which was not treated systematically, all the other *Sciuroides* species which he put in the Sciuroidinae are, according to Bosma (1974), referrable to *Paradelomys*; see details below. Only one of Hartenberger's diagnostic features for the two subfamilies allows comparison: the size of the anterior palatal foramina, and here there is much overlap.

From Hartenberger's (1973) text-fig. 2, only one lineage in his Theridomyidae is shown to have evolved from truly brachyodont to hypsodont and thus bridged his 'Pseudosciuridae'/'Theridomyidae' grade boundary. This is the *Estellomys–Oltinomys* lineage.

The principle of evolution of high-crowned from low-crowned forms is not in doubt here. It is a common and well documented trend among fossil mammals. Even if this happened in parallel, however, no forms originally placed in the Pseudosciuridae have necessarily given rise to any originally placed in the Theridomyidae. Problems in classification always occur when the stem of two suprageneric groups such as these is approached. It is not necessarily solved, however, by lumping the two groups. In post-Bartonian time there are two well-defined groups which differ considerably in crown height and must have occupied very different ecological niches. It seems desirable to recognize these as different families and seek more reliable characters to define each. Three combined features which characterize all the higher-crowned forms plus *Estellomys* are: 1, a mesoloph which tends to join the hypocone; 2, absence of a metalophule I; and 3, an oblique ectolophid without mesoconid. Conversely the Pseudosciuridae have lesser or greater tendencies towards: 1, mesoloph not joined to hypocone; 2, presence of metalophule I independent of the mesoloph; and 3, presence of mesoconid.

The characters outlined above support the retention of these two families, but pose problems for *Paradelomys* and *Tarnomys* which are somewhat intermediate. All the species except typical *P. crusafonti* have a metalophule I, although in the late forms (*P. spelaeus* and *T. quercinus*) it sometimes partially fuses with the mesoloph (see Schmidt-Kittler 1971*a*: fig. 27). However, the earliest assemblage known of *P. crusafonti* (that of Grisolles) has a metalophule I and a short mesoloph. It is evident that the long, but weak, mesoloph which joins the hypocone in assemblages from Robiac times onward is formed by fusion of the short buccal mesoloph to the lingual half of metalophule I, with abortion of the distobuccal half of metalophule I. All the theridomyids may also have undergone a similar modification and the genera here attributed to the Pseudosciuridae may be only those that retained it as a primitive feature. Nevertheless, unlike *P. crusafonti*, typical theridomyids all show a strong hypocone-joining mesoloph. This is more likely to have been derived from a morphology like that occurring in Lutetian *Protadelomys alsaticus* Hartenberger 1969. Some individuals of this species (Hartenberger 1969: pl. 2, figs 4, 7) have a long, strong mesoloph joining the metaconule, which suggests a trend towards the Theridomyidae as construed here.

Paradelomys as defined by its type species alone, *P. crusafonti*, had developed its deep sinus by at least the Bartonian, but still had an oblique ectolophid and no anterolophulid or mesoconid. Three other species that have been referred to *Paradelomys* (*P. depereti*, *P. quercyi* and *P. spelaeus*) have a metalophule I, non-oblique ectolophid, weak mesoconid, antesinusid and anterolophulid. They might usefully be placed in a new genus.

None of the brachyodont theridomyoids that developed metalophule I are known to have given rise to hypsodont taxa, but all that instead developed a strong mesoloph–hypocone link did give rise to hypsodont taxa. This tends to justify the retention of both families as probably monophyletic natural adaptive groups. If it should be found, however, that the characters used to differentiate them were independently evolved, then a modifed system of Hartenberger's subfamilies might prove to be a suitable solution, or different characters again might be used to differentiate the two families.

Family **PSEUDOSCIURIDAE** Zittel 1893

TYPE GENUS. *Pseudosciurus* Hensel 1856.

INCLUDED GENERA. *Protadelomys* Hartenberger 1968, *Sciuroides* Major 1873, *Treposciurus* Schmidt-Kittler 1970, *Suevosciurus* Dehm 1937, *Paradelomys* Thaler 1966 and *Tarnomys* Hartenberger & Schmidt-Kittler 1976.

RANGE. Lutetian to Stampian; England, Belgium, France, Spain, Switzerland and West Germany.

EMENDED DIAGNOSIS. Cheek teeth brachyodont; uppers with metalophule I and/or with rugose to reticulate enamel and only short mesoloph; lowers with mesoconid and/or with bent ectolophid.

TAXONOMIC TREATMENT. Pseudosciurids are represented at Creechbarrow by single species of *Sciuroides*, *Treposciurus* and *Suevosciurus*. They are abundant as individuals and the *Suevosciurus* comprises more than 20% of the total mammal fauna. Because of the varied generic and specific combinations which have been proposed within this family, the maximum number of available characters has been used in a stratigraphical context to minimize the confusing effects of evolutionary reversals and parallelisms. Often these characters are not present in all individuals, infraspecific variation being high. Their percentage occurrences are tabulated in order, to avoid as much as possible use of imprecise words like 'usually' and 'most', which however still need to be used in the generic diagnoses. Equally important as a taxonomic method in the face of such large morphological variation is the estimation of coefficients of size variation. In any one assemblage low coefficients of variation for tooth size give confident species limits (see Gingerich 1974).

DENTAL NOMENCLATURE (Text-fig. 31). Bosma (1974: 16–17) stated that she was following Wood & Wilson (1936) for her nomenclature of the dental pattern. She did not in fact closely follow these authors, possibly because their terminology was designed for only cricetid, heteromyid and sciuravid, not theridomyoid, teeth. Moreover, in Bosma's (1974) text-fig. 2, of a labelled pseudosciurid right upper molar, some of the cusp names have been transposed as if the tooth were a left. These errors are repeated in Bosma & Insole (1976: 2, text-fig. 1). Hartenberger (1973: 6) stated that he was directly following Wood & Wilson (1936) and Schaub (1958) (the latter presumably only for the higher crowned types), but his system differs somewhat from that of Bosma and more closely resembles that of Wood & Wilson for a cricetid type of tooth. I essentially follow Wood & Wilson's and Hartenberger's schemes with the following exceptions:

1, I use paraconule instead of protoconule to maintain uniformity of nomenclature for all mammals with this cusp. The choice is because the paraconule has the same spatial relationship to the paracone, not to the protocone, as the metaconule has to the metacone. 2, I tentatively recognize a mesocone. 3, Bosma (1974) named the loph joining the metacone to the hypocone the metaloph, and the intermediate conule on it the metaconule. The more mesial parallel loph she called metalophule I, from Wood & Wilson (1936). Hartenberger used Wood & Wilson's term metalophule II for Bosma's metaloph but retaining her meaning of metaconule. In post-Lutetian pseudosciurids, there are often two distal lophules on upper molariform teeth, which can be homologized or at least compared for identity of position with metalophules I and II of the cricetid type (Wood & Wilson 1936: 389, fig. 1). Both or either may bear or be reduced to a conule. Of these only the more distal one has been named – the metaconule. In Lutetian pseudosciurids and the presumed ancestral paramyids with tribosphenic teeth, there is a single cusp occasionally on a single crest between metacone and protocone. It can easily be homologized with the metaconule. Individual variation in this region in species of *Protadelomys* as illustrated by Hartenberger (1969) shows incipient development of two lophules and two conules, all derived from or developed around the original metaconule. Therefore metaconule 1 herein is the previously unnamed cusp on or replacing metalophule I, whilst metaconule 2 is the metaconule of Bosma and Hartenberger. 4, I tentatively recognize a hypostyle as the swelling on the posteroloph. 5, the enamel bridge which sometimes links metalophule II to the

posteroloph I name the hypolophule. 6, The crest, which sometimes trends distobuccally from the protocone, I consider can be referred to an incipient protolophule II. 7, I recognize the anterolophulid as used by Mein & Freudenthal (1971: 3) for cricetid teeth.

Development of metalophule I. There is variation in the position of the lingual attachment of metalophule I in pseudosciurids. The condition in upper first and second molars is as follows. In *Sciuroides* it ranges between the lingual half of metalophule II and half way between the middle of the endoloph and the hypocone. In *Treposciurus*, it ranges between the middle of the endoloph and half way between this point and the hypocone. In *Suevosciurus* (vestigially), *Tarnomys* and *Paradelomys* it is predominantly close to or immediately distal to the middle of the endoloph. In DP^4, the lingual attachment in all these genera has the same range as in the M^{1-2} of *Sciuroides*. *Pseudosciurus* has no metalophule I. Late members of the respective genera tend to have a lingual attachment intermediate between the hypocone and the middle of the endoloph, whereas in early members it is at opposite extremes away from this position. Thus there appears to be a time-linked trend towards the intermediate position as the 'optimum'; and a slightly different mode of origin of an otherwise homologous structure.

It appears therefore that, in M^{1-2} of *Sciuroides* and in DP^4 of all the genera, the metaloph begins to split from the buccal end. It is not until the split has progressed right to the endoloph that the 'optimal' position is reached. Some support for this hypothesis is provided by *Protadelomys lugdunensis* Hartenberger 1969, from the Auversian of Lissieu and shown by Hartenberger (1969) to be closely related to *Sciuroides* (under the name of *Suevosciurus*). *P. lugdunensis* has an undivided metaconule but two crests link it to the metacone and only one to the hypocone (Hartenberger 1969: pl. 4, figs 2–3).

Metalophule I in M^{1-2} of the other genera appears to have developed as a crest along the line of the postprotocrista, as the metaconule split in response to the expansion of the distolingual portion of the tooth. That this may have developed fairly rapidly from a morphology closely resembling that of *Protadelomys cartieri* from the late Lutetian of Egerkingen γ (see Hartenberger 1969: pl. 1, fig. 1) is suggested by an unusual individual within the morphologically very variable assemblage of *Treposciurus helveticus preecei* from Creechbarrow. This $M^{1/2}$ (Pl. 18, fig. 8) has no metalophules but a single massive metaconule in a position which would be intersected by a straight line drawn between the protocone and metacone. It is thus slightly more mesial than the metaconule in *P. lugdunensis*. Other variants show different grades of development of the metalophules, mainly I, which nearly always either joins, or is very close to, the middle of the endoloph, where a mesocone is often present.

Thus the most primitive genus in the Pseudosciuridae (*Protadelomys*) lacks metalophule I and could be regarded as providing potential ancestors for both theridomyoid families. As discussed above, important characters are shared between *P. alsaticus* and typical Theridomyidae and between *P. lugdunensis* and typical Pseudosciuridae. More specimens from Lutetian–Auversian sites may eventually result in the splitting up of the genus *Protadelomys*, but it is here provisionally retained undivided within the Pseudosciuridae.

Note on enamel wrinkling. A character of frequent occurrence in the Pseudosciuridae is wrinkling of the enamel. Even at their strongest the wrinkles are not dentine-cored and have often been removed by natural tooth wear. Their pattern may vary, from isolated granules, to a series of ridges, to reticulation. They have been mapped in detail for *Pseudosciurus* by Schmidt-Kittler (1971*a*). The wrinkling may be coarse to fine, low or high, extensive or restricted to only some areas of the tooth. Complicated as they may seem these various features are directly related to the intensity of the wrinkling. Slight wrinkling (grade 1 of the character analysis tables 14–15, 17–18, 20–21) produces low, isolated granules; more intense wrinkling (grade 2) produces a system of ridges; and the maximum observable intensity (grade 3) produces a high reticulate pattern which fills the tooth valleys, leaving deep circular cavities between. Fineness and coarseness vary independently of these grades and together with wear make objective comparisons difficult, but they are nevertheless attempted for the three pseudosciurids from Creechbarrow and their relatives.

Identification of isolated preultimate molars. Isolated first and second molars are difficult to distinguish from one another, but those uppers with near square outline are regarded as M^1 and those with distally tapering outline as M^2; mesially tapering lowers are identified as M_1 and those which are rectangular as M_2. These identifications are only tentative and are attempted for the purposes of the percentage character analysis tables only, where expression of characters in each tooth morphology is important. In the tables and graphs of length and width measurements they are not separated, but nevertheless still produce sufficiently low coefficients of variation.

Genus *SCIUROIDES* Major 1873

Type species. *Sciurus siderolithicus* Pictet & Humbert 1869. Marinesian fissure filling, Eclépens-Gare, Canton Vaud, Switzerland.

Included species. *S. russelli* (Hartenberger & Louis 1976), *S. ehrensteinensis* Schmidt-Kittler 1971*a* and *S. rissonei* sp. nov.

Range. Marinesian; England, France, Switzerland. Ludian; England, Switzerland and ?France.

Emended diagnosis. Upper cheek teeth with: high endoloph; strong, dentine-cored, complete to incomplete metalophule I; strong paraconule; presence of a metaconule 2; DP^4 with straight mesiolingual margin and unicuspid parastyle. Lower cheek teeth with: high, complete, straight oblique to bent ectolophid joining hypolophulid separately from hypoconid; weak mesoconid. Lower molars with: small to large, often median anteroconid on M_{1-2}; anterolophulid usually present; anterolophid weak; metalophulid low and incomplete. DP_4 with: crown height lower than that of molars; metalophulid absent. M_3 hypolophulid high and complete. Anterior palatine foramina project just posterior to maxillary–premaxillary suture (known only for *S. siderolithicus*).

Previous diagnoses. Major (1873) gave no formal diagnosis and Schlosser (1884: 76–77) was the first to give an adequate description. Major's concept of the genus included species now included in other pseudosciurid genera (see Dehm 1937; Schmidt-Kittler 1971*a*). Schmidt-Kittler (1971*a*: 29) gave a brief history of treatment of the genus and a comprehensive diagnosis.

Hartenberger (1973: 21) did not discuss Schmidt-Kittler's diagnosis or concept of *Sciuroides*, but gave his own short diagnosis: 'Crête longitudinale joignant protoconide et hypoconide assez développée. Présence presque constante aux molaires supérieures d'un metalophule I'. Thus his own new species, *Suevosciurus* (*Treposciurus*) *romani*, fits this diagnosis and is in fact inseparable from the type species of *Sciuroides*. Hartenberger included in *Sciuroides* (apart from the type species) '*S.*' *quercyi*, '*S. intermedius*' and '*S.*' *ruetimeyeri*. He incorporated *Sciuroides* and *Paradelomys* into his subfamily Sciuroidinae. One of his characters of this subfamily was medium to large anterior palatine foramina. '*S.*' *quercyi* and '*S. intermedius*' (= '*Paradelomys*' *depereti*, see Bosma 1974: 54) fit the medium category; those of '*S.*' *ruetimeyeri* are unknown; and those of the type species of *Sciuroides* are short and thus prevent its inclusion in the type subfamily.

In contrast, Schmidt-Kittler's (1971*a*) concept of *Sciuroides* produces no anomalies and *Suevosciurus russelli* Hartenberger & Louis 1976 can readily be accommodated in it. Slight emendations and additions are made above and involve the following points. 1. Schmidt-Kittler (1971*a*: 29 and table 4) distinguished *Sciuroides* from the other pseudosciurid genera by the absence of enamel wrinkling. This was based on the few available specimens of *S. siderolithicus* and the unique $M^{1/2}$ of *S. ehrensteinensis*. Bosma (1974: 32–33) described further material of the latter from the Headon Beds of the Isle of Wight and noted that the enamel was slightly rugose. In some individuals of all four species there may be minor unnamed crests branching from the major lophs as well as numerous irregularities of the enamel but they tend to be coarser than those which occur in *Treposciurus* or *Suevosciurus*. Enamel wrinkling is thus not of generic significance. 2, The weakness of the anterolophid and metalophulid is an important character not previously mentioned.

Excluded species. 1. *Adelomys* (*Sciuroides*) *fontensis* Thaler 1966, from the early Ludian of Fons 1. Schmidt-Kittler (1971*a*: 35) thought it was probably synonymous with *S. siderolithicus*. Hartenberger (1973: 29) doubted that it was even a pseudosciurid. It has the interrupted metalophulid of *Sciuroides* and is about the size of *S.* aff. *siderolithicus* from Weidenstetten. Without more material its status is problematical.

2. *Suevosciurus* (*Treposciurus*) *romani* Hartenberger 1973, from the late Bartonian of Robiac. Bosma (1974: 33) put it in *Sciuroides*. Comparison of casts of Hartenberger's figured specimens with the type series of *S. siderolithicus* and referred material from the Quercy Phosphorites in the BM(NH) has shown no tangible differences. UM RBN900 (P^4–M^1 according to Hartenberger 1973: pl. 2, fig. 1) is reidentified as DP^4–M^1 because of the large parastyle and distinct paraconule of the DP^4. The species is here synonymized with *S. siderolithicus* and the Robiac specimens are considered good confirmatory evidence of the Bartonian age of Eclépens-Gare.

3. *Sciuroides intermedius* Schlosser 1884. Schmidt-Kittler (1971*a*) placed this species in his genus *Treposciurus*. The material which Hartenberger (1973: 22) referred to *S. intermedius* is *Adelomys depereti* Stehlin & Schaub 1951 (see Bosma 1974: 54).

4. and 5. *Adelomys depereti* Stehlin & Schaub 1951 and *Sciuroides quercyi* Schlosser 1884. Bosma (1974: 55) placed both in *Paradelomys*. They cannot be *Sciuroides* because they have a deep mesially-directed sinus and its closure buccally (when present) can be shown to be composed of the lingual end of metalophule I fused with incipient protolophule II. This closure is thus not homologous with the strong shallowly-indented endoloph of *Sciuroides*.

6. *Sciurus ruetimeyeri* Pictet & Humbert 1869. This species was referred by Hartenberger (1973: 21) to *Sciuroides*. Schmidt-Kittler (1971*a*: 72–73) thought it should go in a genus of its own while retaining it as '*Sciuroides*' *rütimeyeri* (sic). As interpreted by the better preserved of the two figured syntypes (Pictet & Humbert 1869: pl. 14, fig. 7) (LGM 40464: LM 2930), it is a species of *Paradelomys* very similar to and possibly conspecific with *P. crusafonti*. The upper molar from Eclépens B identified by Schmidt-Kittler (1971*a*: text-fig. 28) as '*Sciuroides*' *rütimeyeri* fits better with *Paradelomys depereti*.

Sciuroides rissonei sp. nov.
(Pl. 15; Text-figs 32–33; Tables 13–15)

v. 1977*b* *Sciuroides* cf. *russelli* (Hartenberger & Louis); Hooker: 141.
v. 1980 *Sciuroides* aff. *russelli* (Hartenberger & Louis); Hooker & Insole: 39.

Name. After Mr A. Rissoné for help with field work.

Holotype. Right $M_{1/2}$ (?M_1), M37386. Pl. 15, fig. 10.

Paratypes. (72): 7 DP^4 (M35532, M36101–4, M37366–7), 3 P^4 (M35539, M36099, M37365), 20 $M^{1/2}$ (M35533–5, M36038, M36105–13, M37368–73, M37699), 8 M^3 (M35537, M36054, M36115–7, M37374–6), 9 DP_4 (M36119–23, M37379–82), 3 P_4 (M36118, M37377–8), 19 $M_{1/2}$ (M35540–5, M36124–33, M37383–5), 3 M_3 (M36134–5, M37700).

Doubtfully referred material. 20 upper incisors (M35579–81, M36136–41, M36175, M37387–95, M37701); lower incisor (M36142).

Type horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Diagnosis. Medium-sized species of *Sciuroides*, mean length of $M^{1/2}$ 2·68 mm. Lingual cusps of upper molars less than twice the height of the buccal cusps; height of buccal cusps of lower molars less than tooth width. Less than 25% of $M^{1/2}$s have metalophule I joining endoloph. 70% of $M_{1/2}$s lack enamel wrinkling. More than 85% of lower premolars and molars have oblique ectolophid which joins hypolophulid between a quarter and a third of the distance from the hypoconid.

Differential diagnosis. *S. russelli* has stongly wrinkled molar enamel. Its lower premolar and molar ectolophids are bent in the middle, the mesial halves being oblique, the distal halves

Plate 15 Scanning electron micrographs of cheek teeth of *Sciuroides rissonei* sp. nov. from Creechbarrow, × 12·5. Fig. 1, right P^4 (reversed) (M36099). Fig. 2, left $M^{1/2}$ (M^1?) (M36106). Fig. 3, right $M^{1/2}$ (M^2?) (reversed) (M36111). Fig. 4, left M^3 (M37374). Fig. 5, left DP^4 (M35532). Fig. 6, right DP^4 (reversed) (M37367). Fig. 7, right $M^{1/2}$ (M^2?) (reversed) (M36107). Fig. 8, right DP_4 (reversed) (M37382). Fig. 9, left P_4 (M36118). Fig. 10, **holotype** right $M_{1/2}$ (M_1?) (reversed) (M37386). Fig. 11, left $M_{1/2}$ (M_2?) (M36128). Fig. 12, left M_3 (M36134). See p. 301.

Table 13 Statistics of length and width measurements of cheek teeth of *Sciuroides rissonei* from the Creechbarrow Limestone Formation, Creechbarrow. (N = number of specimens; OR = observed range; $\bar{x}$ = mean; s = standard deviation; v = coefficient of variation (in brackets where N is too few for v to be significant). See p. 194.

	Length					Width				
Tooth	N	OR	$\bar{x}$	s	v	N	OR	$\bar{x}$	s	v
DP^4	6	2·45–2·75	2·577	0·1203	4·67	7	2·20–2·75	2·414	0·1725	7·15
P^4	2	2·50–3·20	2·850	0·4949	(17·36)	3	2·60–3·00	2·767	0·2082	(7·52)
$M^{1/2}$	17	2·50–2·95	2·682	0·1030	3·84	17	2·65–3·10	2·806	0·1116	3·98
M^3	8	2·40–2·90	2·631	0·1438	5·47	8	2·30–2·90	2·531	0·1811	7·16
DP_4	7	2·45–2·75	2·521	0·1075	4·26	8	1·70–2·20	1·856	0·1568	8·45
P_4	3	2·80–2·95	2·867	0·0764	(2·67)	3	2·00–2·40	2·267	0·2309	(10·19)
$M_{1/2}$	16	2·55–2·90	2·775	0·1096	3·95	16	2·25–2·50	2·366	0·0831	3·51
M_3	2	3·20–3·25	3·225	0·0354	(1·10)	2	2·40–2·55	2·475	0·1061	(4·29)

(with the mesoconid) parallel with the buccal border of the tooth. The ectolophid joins the hypolophulid slightly nearer the hypoconid.

Note that Hartenberger & Louis (1976) recognized this species as congeneric with '*Suevosciurus romani*' but did not realize that both belong in the genus *Sciuroides*. Their diagnosis reflects this: '*Suevosciurus* légèrement plus petit que *S. mutabilis*. D4 et P4 inférieures et supérieures peu molarisées'. In fact *S. russelli* is slightly larger than the type assemblage of *Treposciurus mutabilis*, according to Schmidt-Kittler's (1971*a*: text-fig. 13) measurements.

S. ehrensteinensis is known from a small number of teeth from the English Headon Beds and the German fissure filling Ehrenstein 1A. It is slightly larger than *S. rissonei* or *S. russelli*, has higher lingual upper cheek tooth cusps and higher buccal and lingual lower cheek tooth cusps. Its metalophule I usually joins the endoloph (*fide* Bosma 1974: 33), and its ectolophids are bent.

S. siderolithicus is slightly smaller and has a bent ectolophid which joins the hypolophulid nearer the hypoconid.

Description. Close relationship between this species and *S. russelli* is reflected in the initial records from Creechbarrow (see synonymy list, p. 301). It is considered, however, that identification of *S. rissonei* as *S. russelli* on this basis would confuse, not clarify. The enamel wrinkling is an important specific character within the genus *Treposciurus* (see p. 308) and is thus also considered important in *Sciuroides*. The obliquity of the ectolophid is a notable primitive character within the family.

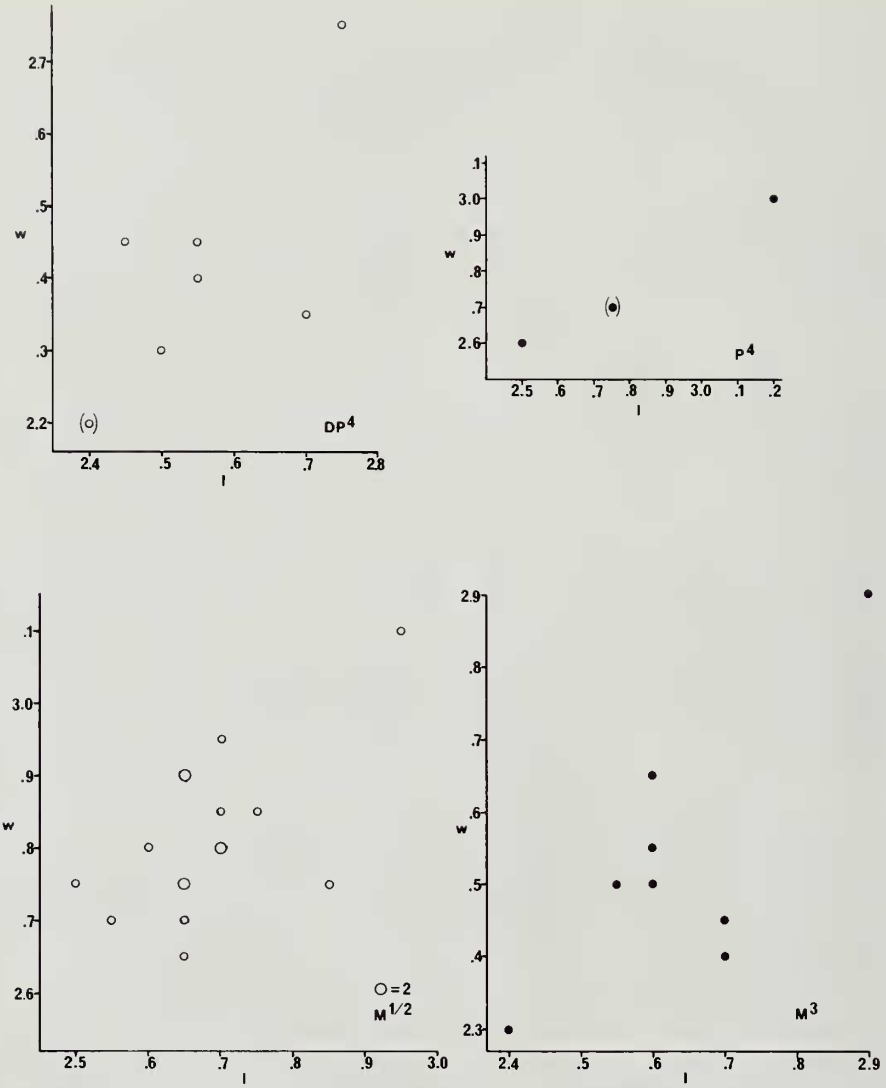
Tables 14–15 show percentage variation of characters for upper and lower cheek teeth. In addition, the paraconule is always large and the endoloph always complete on upper cheek teeth. Not all the incidences of characters are random. There is an 80% correlation between either one of metalophules I and II being broken and the other being complete in $M^{1/2}$. Fifteen specimens are involved. In one specimen (M37699) both I and II are almost broken. Two specimens (M36112 and M36038) have both I and II broken, but in addition have extra unnamed lophules. In M35535 metalophule II looks complete but is separated from the hypocone and joined to the lingual end of the posteroloph by a hypolophule. Pl. 15, figs 2–3 show metalophule I broken and metalophule II complete, while in fig. 7 the condition is reversed. Pl. 15, figs 5 and 6 show variations in shape and size of the parastyle in DP^4. Pl. 15, figs 10–11 show grade 1 enamel wrinkling, while fig. 12 shows grade 2 wrinkling. Unlike *S. ehrensteinensis* from the Isle of Wight (Bosma 1974: pl. 4, fig. 2) no mesostylids are present on any of the Creechbarrow teeth and only a faint ectostylid on one M_3. *S. russelli* M_3s sometimes have a crest joining the hypolophulid to the posterolophid; in *S. rissonei* there is one M_1 and one DP_4 where a projection distally from the hypolophulid fails to join the posterolophid. The interruption of the metalophulid is a good generic feature. There are two individual $M_{1/2}$s, however, where this crest is complete, but in both the anterolophulid is missing.

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Metalophule I joins lingually: metalophule II lingual to metaconule 2 (1), hypocone (2), distal endoloph (3) (7) (3) (8) (10) (0)	1	29	0	25	20	
	2	71	100	50	60	
	3	0	0	25	20	
Metalophule I broken/unbroken (7) (3) (7) (10) (0)	B	86	66·7	57	40	
	U	14	33·3	43	60	
Metalophule II broken/unbroken (7) (3) (6) (10) (6)	B	57	33·3	50	60	33·3
	U	43	66·7	50	40	66·7
Enamel wrinkling (0–3) (7) (3) (7) (10) (6)	0	100	0	100	50	33·3
	1	0	0	0	50	33·3
	2	0	33·3	0	0	33·3
	3	0	66·7	0	0	0
Mesostyle size (0–4) (7) (2) (8) (10) (6)	0	0	0	0	0	16·7
	1	0	0	0	0	0
	2	0	0	13	20	0
	3	86	100	25	80	33·3
	4	14	0	62	0	50
Mesostyle saliency: prominent (3), slight (2), non (1), ectoflexus (0) (7) (2) (5) (9) (7)	0	57	50	0	0	0
	1	43	50	40	22·2	43
	2	0	0	60	66·7	43
	3	0	0	0	11·1	14
Mesostyle mesiodistally elongated (7) (2) (4) (8) (5)	0	85·7	0	75	62·5	20
	1	14·3	100	25	37·5	80
Mesoloph length (0–3) (7) (3) (7) (9) (7)	0	0	0	0	0	14·2
	1	28·6	100	0	22·2	42·9
	2	57·1	0	100	77·8	42·9
	3	14·3	0	0	0	0
Protolophule I broken/unbroken (6) (3) (8) (10) (7)	B	16·7	66·7	0	30	28·6
	U	83·3	33·3	100	70	71·4
Metaconule 2 presence/absence (7) (2) (8) (9) (0)	0	0	50	0	0	
	1	100	50	100	100	
Hypolophule absent (0), partial (1), complete (2) (7) (2) (7) (9) (0)	0	85·7	0	85·7	66·7	
	1	14·3	50	14·3	22·2	
	2	0	50	0	11·1	
Posteroloph broken/unbroken lingually (7) (3) (7) (9) (0)	B	42·9	0	28·6	11·1	
	U	57·1	100	71·4	88·9	
Mesocone presence/absence (7) (3) (8) (10) (7)	0	85·7	100	50	100	57·1
	1	14·3	0	50	0	42·9
Sinus depth: shallow (1) to deep (4) (7) (3) (8) (10) (8)	1	0	0	0	0	0
	2	100	33·3	37·5	0	25·0
	3	0	66·7	25	80	62·5
	4	0	0	37·5	20	12·5
Protostyle presence/absence (6) (2) (7) (10) (8)	0	100	50	14·3	40	75
	1	0	50	85·7	60	25
Hypostyle presence/absence (7) (3) (8) (10) (0)	0	28·6	100	0	30	
	1	71·4	0	100	70	

Tables 14–15 Percentage character analysis of upper (Table 14) and lower (Table 15) cheek teeth of *Sciuroides rissonei* from Creechbarrow. 'Scoring units' give states for characters described in the left hand column. The numbers given under the tooth-headed columns on the right are percentages and refer to the number of teeth showing that particular character state. The lowest row of figures in the left hand column are the respective numbers of each tooth represented. See also p. 303.

Characters + (N) of representative teeth	Scoring units	DP_4	P_4	M_1	M_2	M_3
Distance along hypolophulid	$<\frac{1}{4}$	12·5	0	30	0	0
from hypoconid of junction	$\frac{1}{4}$	50	0	70	30	100
with ectolophid	$\frac{1}{3}$	37·5	33·3	0	70	0
(8) (3) (7) (10) (2)	$\frac{3}{8}$	0	33·3	0	0	0
	$\frac{3}{8}-\frac{1}{2}$	0	33·3	0	0	0
Orientation of ectolophid:	SO	43	100	57	90	100
straight oblique/bent parallel	BP	57	0	43	10	0
(7) (3) (7) (10) (2)						
Anteroconid size (1–3)	1			30	40	0
(0) (0) (7) (10) (2)	2			40	30	50
	3			30	30	50
Anterolophulid absent (0), weak	0			15	23·3	50
(1), strong (2)	1			42	33·3	50
(0) (0) (7) (10) (2)	2			43	43·3	0
Mesoconid length as % depth	0	0	66·7	0	0	0
of sinusid	40	0	0	0	10	0
(6) (3) (7) (10) (2)	50	33·3	33·3	29	10	50
	60	33·3	0	29	30	50
	70	33·3	0	21	15	0
	80	0	0	21	35	0
Mesolophid absent (0), $\frac{1}{4}$ complete	0	60	100	70	40	0
(1), $\frac{1}{2}$ complete (2)	1	15	0	15	40	100
(8) (3) (7) (10) (2)	2	25	0	15	20	0
Enamel wrinkling (0–2)	0	85	0	57	70	50
(8) (3) (7) (10) (2)	1	0	66·7	43	20	0
	2	15	33·3	0	10	50
Mesostylid presence/absence	0	100	100	100	90	100
(8) (3) (7) (10) (2)	1	0	0	0	10	0
Ectostylid presence/absence	0	100	100	100	100	50
(8) (3) (7) (10) (2)	1	0	0	0	0	50
Hypoconulid presence/absence	0	15	33·3	57	60	50
(8) (3) (7) (10) (2)	1	85	66·7	43	40	50
Distal crest to hypoconulid	0	87·5	100	14·3	100	100
presence/absence	1	12·5	0	85·7	0	0
(8) (3) (7) (10) (2)						

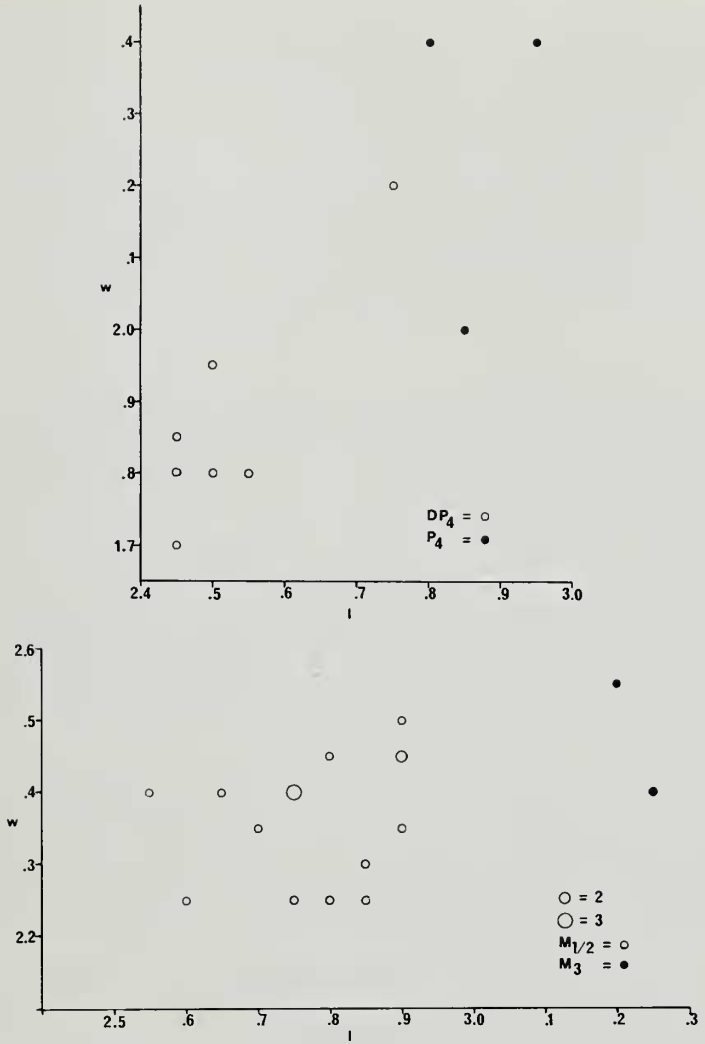
PHYLOGENETIC RELATIONSHIPS. Schmidt-Kittler (1971*a*) considered that there were three valid species of *Sciuroides*: *S. siderolithicus*, *S. ehrensteinensis* and *S.* sp. A. For him, *S. siderolithicus* gave rise to *S.* sp. A whereas *S. ehrensteinensis* was on a separate lineage. Bosma's (1974: 33) new material of *S. ehrensteinensis* indicated to her that *S.* sp. A fell within its range of variation.



Text-figure 32 Scatter diagrams of length (l) against width (w) in DP^4, P^4, $M^{1/2}$ and M^3 of *Sciuroides rissonei* sp. nov. from Creechbarrow. Measurements in millimetres.

Subsequently the discoveries of *S. russelli* and *S. rissonei* from the Bartonian provide more potential candidates for the ancestry of *S. ehrensteinensis*. In the sum of its characters, *S. rissonei* is the most primitive species of *Sciuroides* and could have given rise to all the others. It is easy to envisage the small changes needed for it to give rise to both *S. russelli* and *S. siderolithicus*; and specimens intermediate in size between *S. siderolithicus* and *S. ehrensteinensis* from Eclépens B and Weidenstetten (*S.* aff. *siderolithicus* of Schmidt-Kittler 1971*a*) give an idea of the probable origin of *S. ehrensteinensis*.

Two important generic characters of *Sciuroides*, the high endoloph and the incomplete metalophulid, are shared with *Protadelomys lugdunensis* from the Auversian of Lissieu. One important character of *P. lugdunensis* is shared with *Sciuroides rissonei*: the oblique ectolophid.



Text-figure 33 Scatter diagrams of length (l) against width (w) in DP_4, P_4, $M_{1/2}$ and M_3 of *Sciuroides rissonei* sp. nov. from Creechbarrow. Measurements in millimetres.

This makes *P. lugdunensis* the best candidate we have for ancestry of the genus *Sciuroides*. The probable mode of development of metalophule I is described above under Pseudosciuridae (p. 299).

Genus ***TREPOSCIURUS*** Schmidt-Kittler 1970

TYPE SPECIES. *T. mutabilis* Schmidt-Kittler 1970. Ludian fissure filling; Ehrenstein 1A, near Ulm, West Germany.

INCLUDED SPECIES. *T. intermedius* (Schlosser 1884) Schmidt-Kittler 1970, *T. helveticus* Schmidt-Kittler 1971*a*, new rank.

RANGE. Marinesian–Ludian; England, France, Spain, Switzerland and West Germany.

EMENDED DIAGNOSIS. Upper cheek teeth with: endoloph low, usually incomplete; metalophule I strong to weak, not dentine-cored (except sometimes at metaconule 1), complete, incomplete or missing, and in M^{1-2} attached to endoloph from near middle to near hypocone; paraconule weak on P^4, strong on DP^4 and M^{1-2}, may be weak on M^3; metaconule 2 present or absent. DP^4 with medium-sized, often bicuspid parastyle and straight mesiolingual margin. Lower cheek teeth with: ectolophid low, complete to incomplete, bent parallel, joining hypolophulid between hypoconid and one-third of the distance from the hypoconid to the entoconid; mesoconid weak to strong. Lower molars with: M_{1-2} anteroconid absent to large, usually buccal to midline; anterolophulid present or absent; anterolophid strong; metalophulid high and complete to low and incomplete. M_3 hypolophulid high to low, usually complete. DP_4 with: crown height lower than that of molars; metalophulid present to absent. Anterior palatine foramina project just posterior to maxillary–premaxillary suture (known for *T. mutabilis* and *T. intermedius*).

Treposciurus helveticus Schmidt-Kittler 1971*a*, new rank

v* 1971*a* *Treposciurus mutabilis helveticus* Schmidt-Kittler: 53–57; pl. 2, fig. 7; text-figs 23–24.
v. *1977b* *Treposciurus* sp.; Hooker: 141.
v. *1980* *Treposciurus* sp.; Hooker & Insole: 39.

TYPES. See under nominate subspecies.

RANGE. Marinesian to early Ludian; England and Switzerland.

EMENDED DIAGNOSIS. M^{1-2} metalophule I not dentine-cored, incomplete to complete, joining endoloph just distal to sinus (at mesocone if present) or nearer hypocone, or may be absent sometimes replaced by fairly strong enamel wrinkling. M_{1-2} with weak enamel wrinkling or just a few strong folds; moderately to strongly developed anteroconid with weak or no anterolophulid and moderate anterolophid; mesoconid usually strong, tending to extend more than half the depth of the sinusid. DP_4 lacks metalophulid.

DIFFERENTIAL DIAGNOSIS. *T. mutabilis*: all cheek teeth possess strong reticulate enamel. M^{1-2} consistently lack any metalophule I. M_{1-2} anteroconid is weak to absent, anterolophulid usually present, anterolophid strong; mesoconid usually weak but often extending as narrow ridge through the sinusid. DP_4 has metalophulid.

T. intermedius: M^{1-2} consistently possess incomplete to complete metalophule I, joining endoloph at or near hypocone. M_{1-2} mesoconid usually weak.

Treposciurus helveticus helveticus Schmidt-Kittler 1971*a*

v* 1971*a* *Treposciurus mutabilis helveticus* Schmidt-Kittler: 53–57; pl. 2, fig. 7; text-figs 23–24.
v. 1971*a* *Pseudosciurus* A n. sp.; Schmidt-Kittler: 29, text-fig. 9.

Table 16 Statistics of length and width measurements of cheek teeth of *Treposciurus helveticus preecei* from Creechbarrow. (Notation as in Table 13, p. 303).

Tooth	Length					Width				
	N	OR	$\bar{x}$	s	v	N	OR	$\bar{x}$	s	v
DP^4	3	2·10–2·27	2·18	0·0854	(3·92)	5	1·87–2·10	1·99	0·1031	5·17
P^4	2	1·77–2·05	1·91	0·1980	(10·37)	2	1·88–2·03	1·96	0·1061	(5·41)
$M^{1/2}$	18	1·95–2·25	2·10	0·0834	3·98	19	1·98–2·28	2·15	0·0946	4·39
M^3	6	1·85–2·13	2·05	0·0972	4·75	5	1·83–2·21	2·06	0·1462	7·10
DP_4	1	1·82	–	–	–	1	1·33	–	–	–
P_4	4	1·93–2·10	2·01	0·0850	(4·23)	4	1·58–1·89	1·72	0·1365	(7·94)
$M_{1/2}$	14	2·05–2·40	2·18	0·0996	4·57	12	1·73–2·10	1·93	0·1093	5·66
M_3	7	2·33–2·71	2·48	0·1337	5·40	7	1·81–2·00	1·91	0·0628	3·28

TYPES AND RANGE. Holotype (LGM 40209) and paratypes from the Sidérolithique, Eclépens (B?), Canton Vaud, Switzerland; teeth in the NMB (referred herein) also from Eclépens B. Schmidt-Kittler (1971*a*: 53–57) only recorded his material as being from Eclépens, but all rodent material from the new fissures was collected from Eclépens B (personal communication, D. Rigassi 1980).

EMENDED DIAGNOSIS. Mean length of $M^{1/2}$ 2·33 mm. Range 2·08–2·64 mm.

Treposciurus helveticus preecei subsp. nov.
(Pl. 16; Pl. 17, figs 1–6; Text-figs 34–35; Tables 16–18)

v. *1977b Treposciurus* sp.; Hooker: 141.
v. *1980 Treposciurus* sp.; Hooker & Insole: 39.

NAME. After Dr R. Preece for help with field work.

TYPES. As the definition of this subspecies is based on a size range which overlaps with the other subspecies, and as its morphological variation is very high, the designation of a holotype is inappropriate. Therefore contrary to Recommendation 73A of the International Code of Zoological Nomenclature (1985: 149), I give all members of this type series equal status in the form of 75 **syntypes**: 6 DP^4 (M36034–7, M36100, M37331), 4 P^4 (M36032–3, M37330, M37337), 25 $M^{1/2}$ (M35509–10, M35512–4, M36039, M36041–53, M36067, M37332–6), 7 M^3 (M35515–8, M36055, M37338–9), 1 DP_4 (M36058), 6 P_4 (M35538, M36056–7, M37340–2), 19 $M_{1/2}$ (M35519–29, M36059–60, M36062–3, M37343–6), 7 M_3 (M35530–1, M36064–6, M37347–8).

DOUBTFULLY REFERRED MATERIAL. 53 upper incisors (M35564–73, M36068–96, M36170–4, M37349–57); 14 lower incisors (M35574–8, M36097–8, M37358–64).

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Mean length of $M^{1/2}$ 2·10 mm. Range 1·95–2·25 mm.

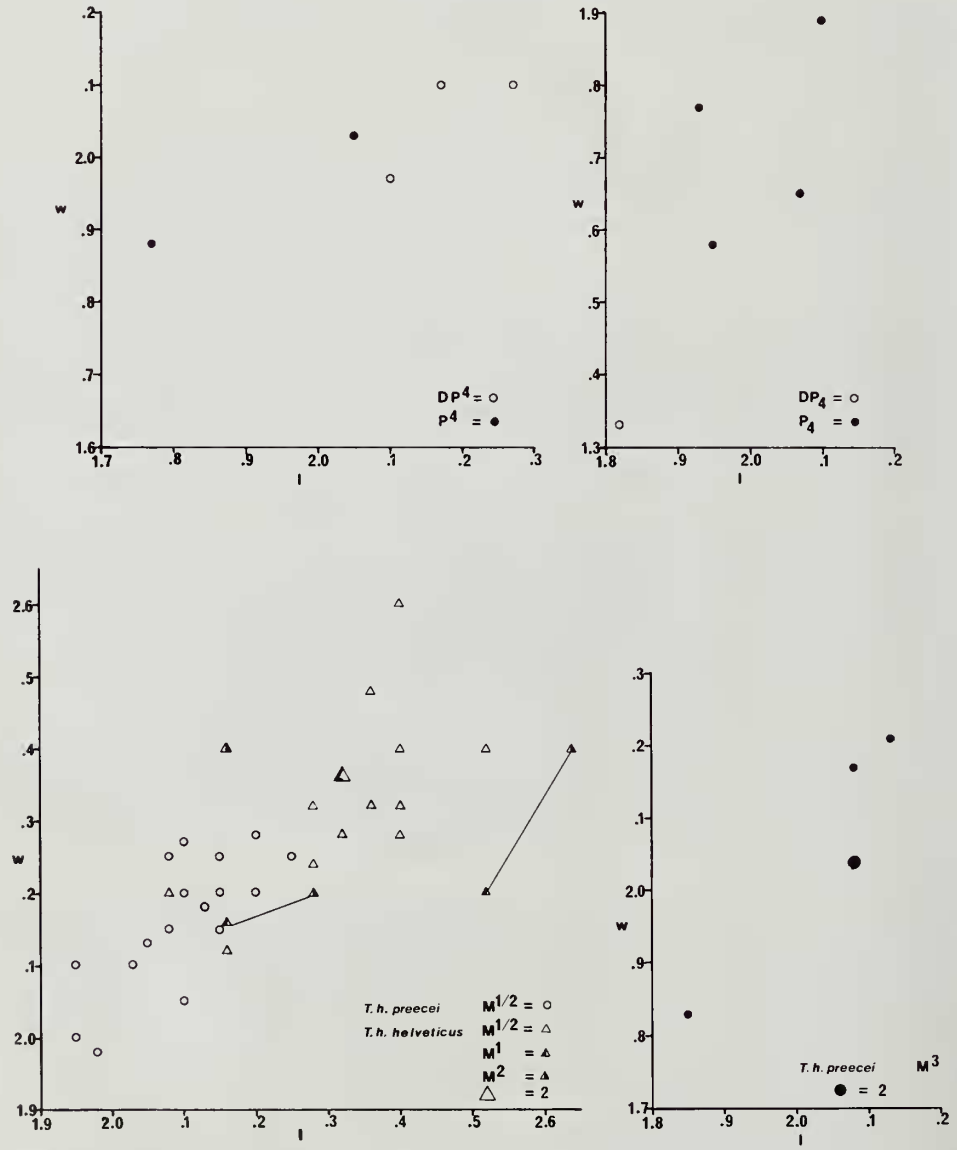
COMMENT ON TAXONOMY. The *Treposciurus* from Creechbarrow is very similar in morphology and range of morphological variation to the type and referred material of *T. mutabilis helveticus* from Eclépens B. The only tangible difference is in the size, it being smaller but with overlapping range. As there are morphological differences between *T. m. helveticus* and *T. m. mutabilis*, especially now that the former is known from more material from the type locality, it is proposed here that the subspecies *T. m. helveticus* be raised to the rank of species.

Material from the Headon and Osborne Beds, referred by Bosma (1974) and Bosma & Insole (1976) to *T. m. helveticus*, is morphologically very similar to *T. m. mutabilis*. It differs only in being slightly smaller, but there is much overlap in measurements. Therefore it is proposed to refer this material to *T. mutabilis* with no division into subspecies. The overlap in size between the Creechbarrow *Treposciurus* and *T. helveticus* Schmidt-Kittler 1971*a*, new rank, from Eclépens B is much less and it is proposed to recognize them as conspecific but belonging to different subspecies.

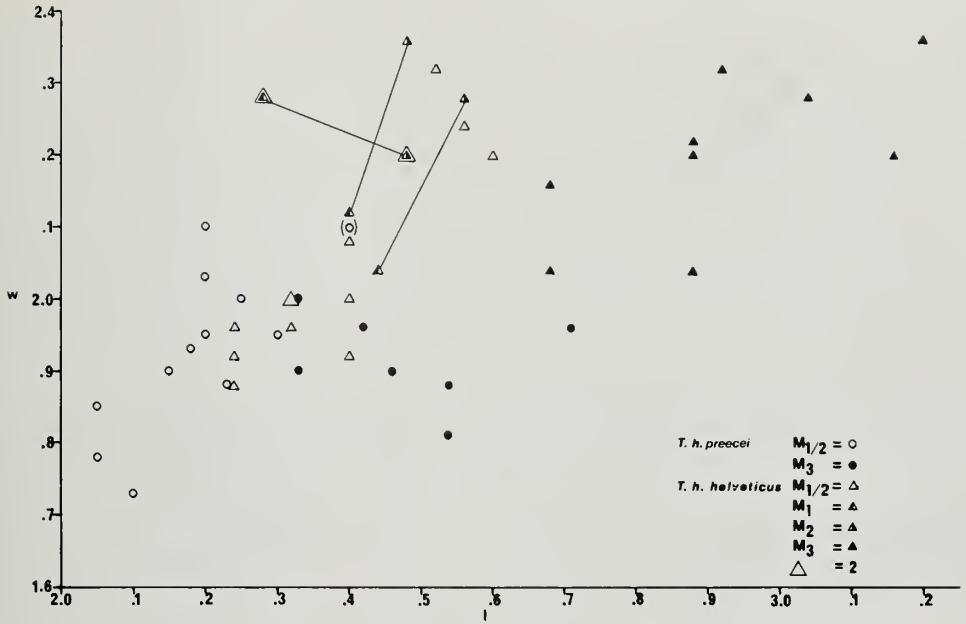
DESCRIPTION. Of the three English Bartonian pseudosciurids, *T. helveticus preecei* is the most variable in morphology, especially in the upper molars. Since two particular morphologies, which characterize respectively *T. mutabilis* and *T. intermedius*, are present at Creechbarrow, it could be doubted that only a single species were represented there. However, the lack of any clear-cut morphological differences on which subdivisions could be made, the unimodal size distribution and its low coefficient of variation (Table 16) especially in the first and second molars, and the presence of similar morphological range in the Eclépens B assemblage of *T. helveticus*, serve to remove doubt.

In Tables 17–18, morphological variation is given as in Tables 20–21 for *Suevosciurus authodon* (pp. 319–321). The major variations in $M^{1/2}$ are illustrated in Pl. 16, figs 2–3, 7, 9–12. Pl. 16, fig. 11 shows a morphology almost identical to that of *T. mutabilis*; the only difference is that the enamel in the centre of the tooth is not quite so strongly or deeply reticulate as is usual for *T. mutabilis*. Fig. 12 shows a morphology almost identical to that of *T. intermedius*; the

replacement of the lingual end of metalophule II by a hypolophule joining the posteroloph is a variant feature which can often occur in any species of *Treposciurus* or *Suevosciurus*. The former tooth is the largest in the assemblage and the latter one of the smallest, thus corresponding to the respective size differences of the Ludian species they resemble. Apart from these extremes there are specimens that show a mainly incomplete metalophule I which usually joins the endoloph just distal to the midpoint, unlike *T. intermedius* where it joins the endoloph



Text-figure 34 Scatter diagrams of length (l) against width (w) in DP^4, P^4, DP_4 and P_4 of *Treposciurus helveticus preecei* subsp. nov. from Creechbarrow, and in $M^{1/2}$ of *Treposciurus helveticus helveticus* Schmidt-Kittler from Eclépens B and $M^{1/2}$ and M^3 of *T. helveticus preecei* from Creechbarrow. Measurements in millimetres. Lines join teeth of one individual.



Text-figure 35 Scatter diagrams of length (l) against width (w) in $M_{1/2}$ and M_3 of *Treposciurus helveticus helveticus* Schmidt-Kittler from Eclépens B and *T. helveticus preecei* subsp. nov. from Creechbarrow. Measurements in millimetres. Lines join teeth of one individual.

nearer the hypocone. Some specimens have smooth enamel and no metalophule I at all and there are complex intermediates between most of these types. Fig. 7 shows a doubled metaconule 2, whilst Fig. 9 shows a single, huge, undivided metaconule such as occurs in the late Lutetian *Protadelomys cartieri* from Egerkingen γ, Switzerland. One very curious $M^{1/2}$ (M35514) is relatively elongated, has no metalophule I, a very shallow sinus and a strong lingual cingulum completely spanning the sinus and rising distally to about a third the crown height of the hypocone.

There is less variation in the lower molars. No $M_{1/2}$s show features typical of *T. mutabilis* and the lower molars of *T. intermedius* have no special distinguishing characters. M35524 is peculiar in having a double mesoconid. An M_3 (M37348) deserves special mention (Pl. 17, fig. 6); unlike the typical shape shown in Pl. 17, fig. 4, its outline is a parallelogram, the acute angles being the mesiolingual and distobuccal corners.

Phylogenetic relationships. From the polymorphic pattern described above it is possible to formulate a phylogenetic model for the three *Treposciurus* species. This involves a cladogenesis with *T. helveticus* as the common ancestor of *T. mutabilis* and *T. intermedius*. The two Ludian species would have developed by selection of different morphs already present in the Bartonian species. The two daughter species are thus more specialized than the ancestral species. This speciation event seems to have occurred at about the Bartonian/Ludian boundary, at a time when there was a widespread marine regression with mammalian migrations and extinctions within Europe (see Garimond *et al.* 1975), thus increasing selection pressures.

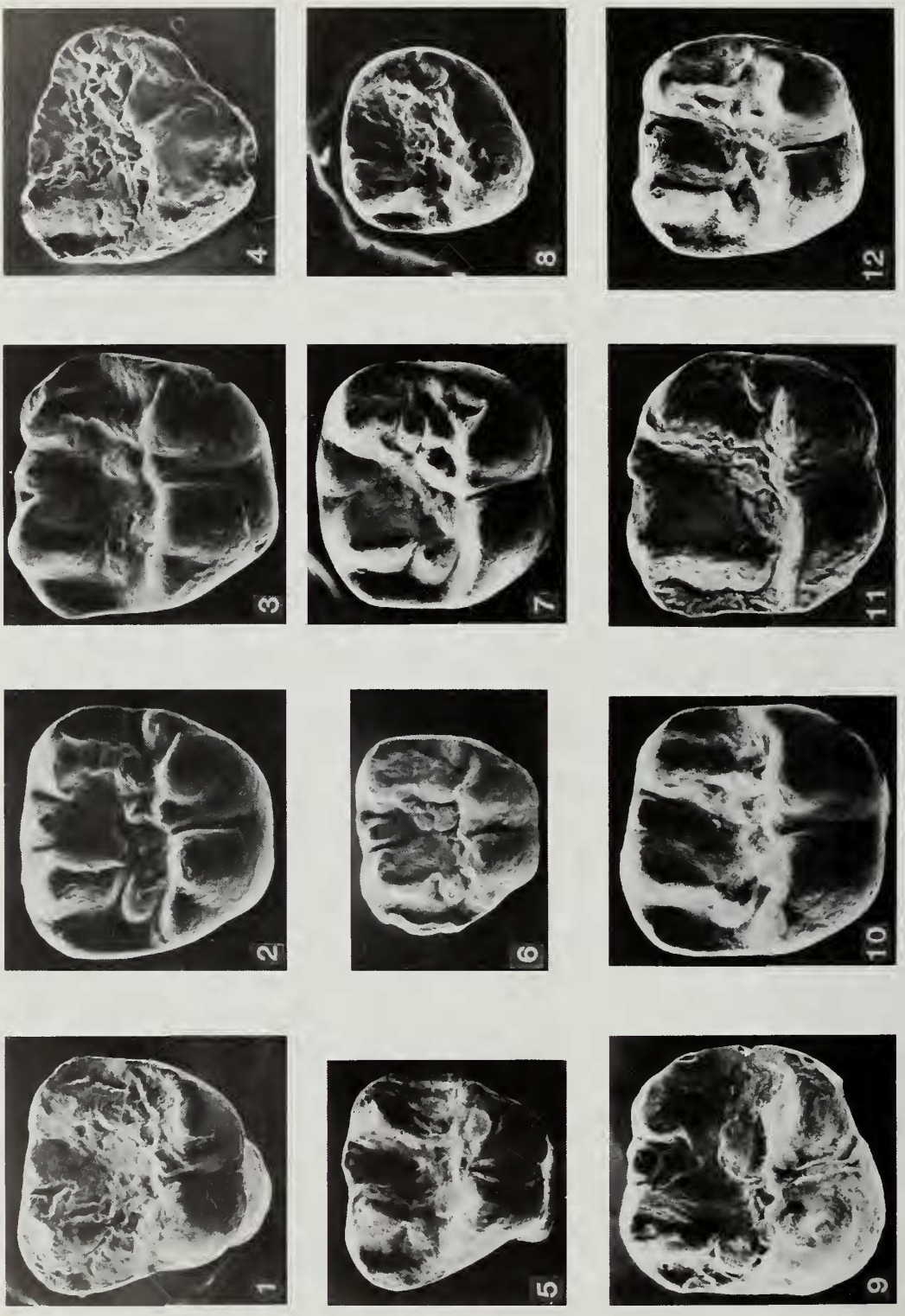
It is not certain whether the differences between the two subspecies of *T. helveticus* reflect geographical or stratigraphical separation. There is some biostratigraphical evidence that Eclépens B is younger than Creechbarrow (see correlation section, pp. 425–427). Alternatively, if the subspecies were geographical, it is possible that *T. intermedius* arose in the region of southern England and *T. mutabilis* in the region of Switzerland.

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Metalophule I joins lingually:	0	0	75	37·5	63·6	
metalophule II lingual to	1	20	0	0	0	
metaconule 2 (1), hypocone (2),	2	80	25	12·5	9·1	
distal endoloph (3), central endoloph (4);	3	0	0	0	18·2	
is absent (0)	4	0	0	50·0	9·1	
(5) (4) (8) (11) (0)						
Metalophule I broken/unbroken	B	60	100	100	90·9	
(5) (4) (8) (11) (0)	U	40	0	0	9·1	
Metalophule II broken/unbroken	B	0	25	50	18·2	75
(5) (4) (8) (11) (4)	U	100	75	50	81·8	25
Enamel wrinkling (0–3)	0	83·3	0	0	12·5	0
(6) (3) (7) (8) (6)	1	0	0	85·7	50·0	0
	2	16·7	33·3	14·3	37·5	0
	3	0	66·7	0	0	100
Mesostyle size (0–4)	0	0	0	0	0	80
(5) (3) (7) (11) (5)	1	0	0	0	0	0
	2	0	66·7	0	9·1	0
	3	80	33·3	100	90·9	0
	4	20	0	0	0	20
Mesostyle saliency:	0	25	0	0	0	0
slight (2), non (1), ectoflexus (0)	1	50	66·7	85·7	100	40
(4) (3) (7) (10) (5)	2	25	33·3	14·3	0	60
Mesostyle mesiodistally elongated	0	100	100	87·5	100	0
(5) (3) (8) (11) (5)	1	0	0	12·5	0	100
Mesoloph length (0–3)	0	20	33·3	25	27·2	100
(5) (3) (8) (11) (5)	1	40	66·7	12·5	18·2	0
	2	20	0	50	45·5	0
	3	20	0	12·5	9·1	0
Protolophule I broken/unbroken	B	0	66·7	75	37·5	20
(5) (3) (8) (8) (5)	U	100	33·3	25	62·5	80
Metaconule 2 presence/absence	0	33·3	0	12·5	80	
(6) (3) (8) (10) (0)	1	66·7	100	87·5	20	
Hypolophule absent (0), partial	0	100	100	87·5	90	
(1), complete (2)	1	0	0	0	0	
(6) (3) (8) (10) (0)	2	0	0	12·5	10	
Posteroloph broken/unbroken lingually	B	50	0	87·5	44·4	
(4) (4) (8) (9) (0)	U	50	100	12·5	55·6	
Mesocone presence/absence	0	100	100	62·5	80	57·1
(6) (4) (8) (10) (7)	1	0	0	37·5	20	42·9
Sinus depth: shallow (1) to	1	0	0	12·5	0	0
deep (4)	2	20	75	37·5	20	14·3
(5) (4) (8) (10) (7)	3	80	25	37·5	50	57·1
	4	0	0	12·5	30	28·6
Protostyle presence/absence	0	20	66·7	62·5	36·4	50
(5) (3) (8) (11) (4)	1	80	33·3	37·5	63·6	50

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Hypostyle presence/absence	0	25	100	25	60	
(4) (4) (8) (10) (0)	1	75	0	75	40	
Paraconule small (1), large (2)	1	0	33·3	0	0	28·6
(6) (3) (8) (11) (7)	2	100	66·7	100	100	71·4
Endoloph broken (1), complete (2)	1	0	25	50	12·5	0
(6) (4) (8) (9) (5)	2	100	75	50	87·5	100
DP^4 parastyle bicuspid	0	66·7				
(3)	1	33·3				

Tables 17–18 Percentage character analysis of upper (opposite and above) and lower (below) cheek teeth of *Treposciurus helveticus preecei* from Creechbarrow. For explanation see Table 14, p. 305.

Characters + (N) of respective teeth	Scoring units	DP_4	P_4	M_1	M_2	M_3
Distance along hypolophulid	$<\frac{1}{4}$	100	25	45·4	50	83·3
from hypoconid of junction	$\frac{1}{4}$	0	75	36·4	50	16·7
with ectolophid	$\frac{1}{3}$	0	0	18·2	0	0
(1) (4) (11) (6) (6)						
Anteroconid size (1–3)	1			40	33·3	50
(0) (0) (10) (6) (6)	2			40	66·7	50
	3			20	0	0
Anterolophulid absent (0), weak	0			87·5	83·3	80
(1), strong (2)	1			12·5	16·7	0
(0) (0) (8) (6) (5)	2			0	0	20
Mesoconid length as % depth of	40	100	0	0	0	0
sinusid	50	0	0	10	0	0
(1) (4) (10) (6) (6)	60	0	0	0	33·3	0
	70	0	25	30	33·3	16·7
	80	0	75	40	16·7	16·7
	90	0	0	10	16·7	66·6
	100	0	0	10	0	0
Mesolophid absent (0), $\frac{1}{4}$ complete (1)	0	100	25	45·5	66·7	50
(1) (4) (11) (6) (6)	1	0	75	54·5	33·3	50
Enamel wrinkling (0–2)	0	100	0	75·0	80	0
(1) (4) (8) (5) (6)	1	0	25	12·5	20	50
	2	0	75	12·5	0	50
Mesostylid presence/absence	0	100	100	70	60	83·3
(1) (4) (10) (5) (6)	1	0	0	30	40	16·7
Ectostylid presence/absence	0	100	100	100	83·3	100
(1) (4) (8) (6) (6)	1	0	0	0	16·7	0
Hypoconulid presence/absence	0	0	50	70	60	66·7
(1) (4) (10) (5) (6)	1	100	50	30	40	33·3
Distal crest to hypolophulid	0	100	100	90·9	100	100
(1) (4) (11) (6) (6)	1	0	0	9·1	0	0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Genus *SUEVOSCIURUS* Dehm 1937

[incl. *Suevosciurus* (*Microsuevosciurus*) Hartenberger, 1973]

TYPE SPECIES. *Sciuroides fraasi* Major 1873. Ludian fissure filling; Örlinger Tal, West Germany.

INCLUDED SPECIES. *S. ehingensis* Dehm 1937, *S. minimus* (Major 1873), *S. palustris* (Misonne 1957) and *S. authodon* sp. nov. Note that Bosma (1974: 53) has removed Hartenberger's (1973: pl. 1, figs 6–13) '*Suevosciurus* aff. *minimus*' from Fons 4 from *Suevosciurus* and compared it with *Treposciurus*.

RANGE. Marinesian–Ludian, England; Ludian–Stampian, W. Germany; Ludian, France and Switzerland; early Stampian, Belgium; Oligocene, Majorca.

EMENDED DIAGNOSIS. Upper cheek teeth with: endoloph high, usually complete; M^{1-2} metalophule I usually missing, occasionally present, not dentine-cored, developed as ridge lingually only or as metaconule 1, in which case usually attached to endoloph just distal to midpoint; paraconule strong to weak on DP^4 and M^{1-3}; metaconule 2 usually absent; DP^4 with medium to large, often bicuspid parastyle and usually concave mesiolingual margin. Lower cheek teeth with: ectolophid complete, but low, to incomplete, bent parallel, joining hypolophulid at or close to hypoconid; mesoconid nearly always strong. Lower molars with: M_{1-2} anteroconid usually large, usually buccal to midline: anterolophulid nearly always absent; anterolophid strong; metalophulid high and complete. M_3 hypolophulid incomplete or low and complete. DP_4^4 with: crown height equal to that of molars; metalophulid present. Anterior palatine foramina project just posterior to maxillary–premaxillary suture (known for *S. fraasi* and *S. ehingensis*).

PREVIOUS DIAGNOSES. The most recent was by Hartenberger (1973: 11), but this reflects his inclusion in the genus of species referable to *Treposciurus* and *Sciuroides* (see discussions under these genera). The diagnosis herein is closer to that of Schmidt-Kittler (1971*a*: 39) but involves the reidentification of his P_4^4 as DP_4^4 and the characters of subsequently described material from the Isle of Wight (Bosma 1974) and Creechbarrow (herein).

Suevosciurus authodon sp. nov.

(Pl. 17, figs 7–12; Pl. 18; Text-figs 36–39; Tables 19–21)

v. *1977b Suevosciurus* sp.; Hooker: 141.
v. *1980 Suevosciurus* sp. 1; Hooker & Insole: 39.

NAME. Noun in apposition, from Greek *αὖθις*, afresh, and *ὀδούς*, tooth, in allusion to the tooth replacement in this species.

HOLOTYPE. Right DP^4, M35469. Pl. 18, fig. 5.

PARATYPES. (336): 27 DP^4 (M35470–1, M35787, M35797–813, M36447, M37205–10); 23 P^4 (M35464–8, M35486, M35785–6, M35788–96, M37199–204); 102 $M^{1/2}$ (M35472–7, M35814–75, M37211–35); 25 M^3 (M35488–90, M35876–88, M37236–44): 2 DP_4 (M35897, M37247); 13 P_4 (M35491–2, M35889–96, M35898, M37245–6); 102 $M_{1/2}$ (M35493–504, M35899–960, M37248–75); 42 M_3 (M35505–8, M35961–87, M37276–86).

DOUBTFULLY REFERRED MATERIAL. 44 upper incisors (M35549–53, M35988–36008, M36161–2, M37287–302); 67 lower incisors (M35554–63, M36009–31, M36163–9, M37303–29).

Plate 16 Scanning electron micrographs of upper cheek teeth of *Treposciurus helveticus preecei* subsp. nov. from Creechbarrow, ×18. All are **syntypes**. Fig. 1, left P^4 (M36032). Fig. 2, left $M^{1/2}$ (M^1?) (M36045). Fig. 3, left $M^{1/2}$ (M^2?) (M36043). Fig. 4, left M^3 (M35516). Fig. 5, left DP^4 (M36100). Fig. 6, right DP^4 (reversed) (M36037). Fig. 7, right $M^{1/2}$ (M^1?) (reversed) (M35513). Fig. 8, right M^3 (reversed) (M35518). Fig. 9, right $M^{1/2}$ (M^2?) (reversed) (M35512). Fig. 10, right $M^{1/2}$ (M^2?) (reversed) (M37334). Fig. 11, right $M^{1/2}$ (M^2?) (reversed) (M36051). Fig. 12, left $M^{1/2}$ (M^2?) (M36039). See p. 309.

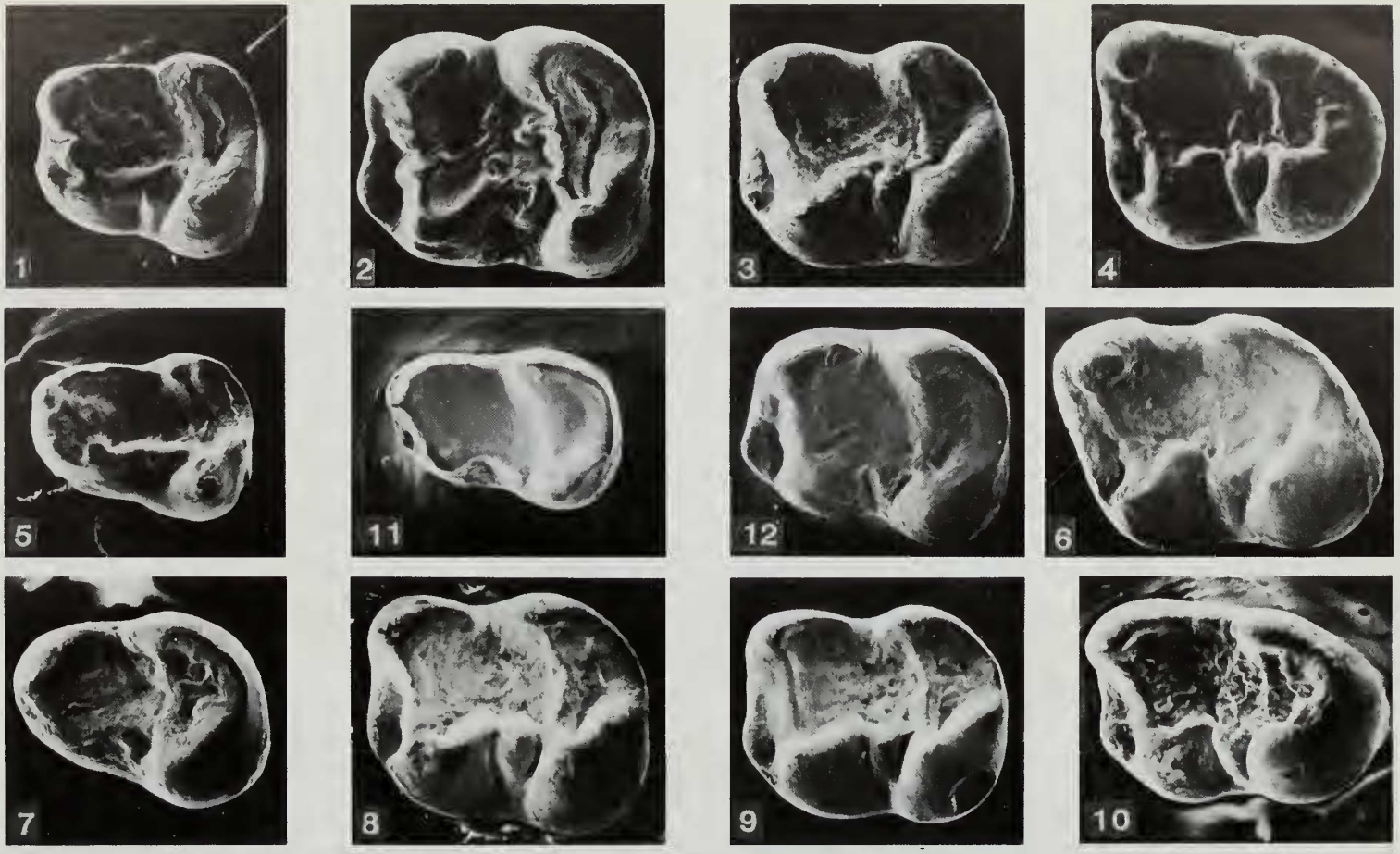


Plate 17 Scanning electron micrographs of lower cheek teeth of *Treposciurus* and *Suevosciurus* from Creechbarrow.

Figs 1–6 *Treposciurus helveticus preecei* subsp. nov., **syntypes**, × 18. Fig. 1, right P_4 (reversed) (M37342). Fig. 2, right $M_{1/2}$ (M_1?) (reversed) (M37346). Fig. 3, right $M_{1/2}$ (M_2?) (reversed) (M37345). Fig. 4, right M_3 (reversed) (M36065). Fig. 5, left DP_4 (M36058). Fig. 6, right M_3 (reversed) (M37348). See p. 309.

Figs 7–12 *Suevosciurus authodon* sp. nov., × 25. Fig. 7, left P_4 (M35891). Fig. 8, left $M_{1/2}$ (M_1?) (M35918). Fig. 9, right $M_{1/2}$ (M_2?) (reversed) (M35926). Fig. 10, left M_3 (M35961). Fig. 11, right DP_4 (reversed) (M35897). Fig. 12, left $M_{1/2}$ (M_1?) (M35907). See p. 315.

TYPE HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Mean length of $M^{1/2}$ 1·49 mm; range 1·350–1·625 mm. $P^{\frac{4}{4}}$ present. DP^4 mean length/width ratio 1·08. 70% $M^{1/2}$s have size 2 metaconule 1.

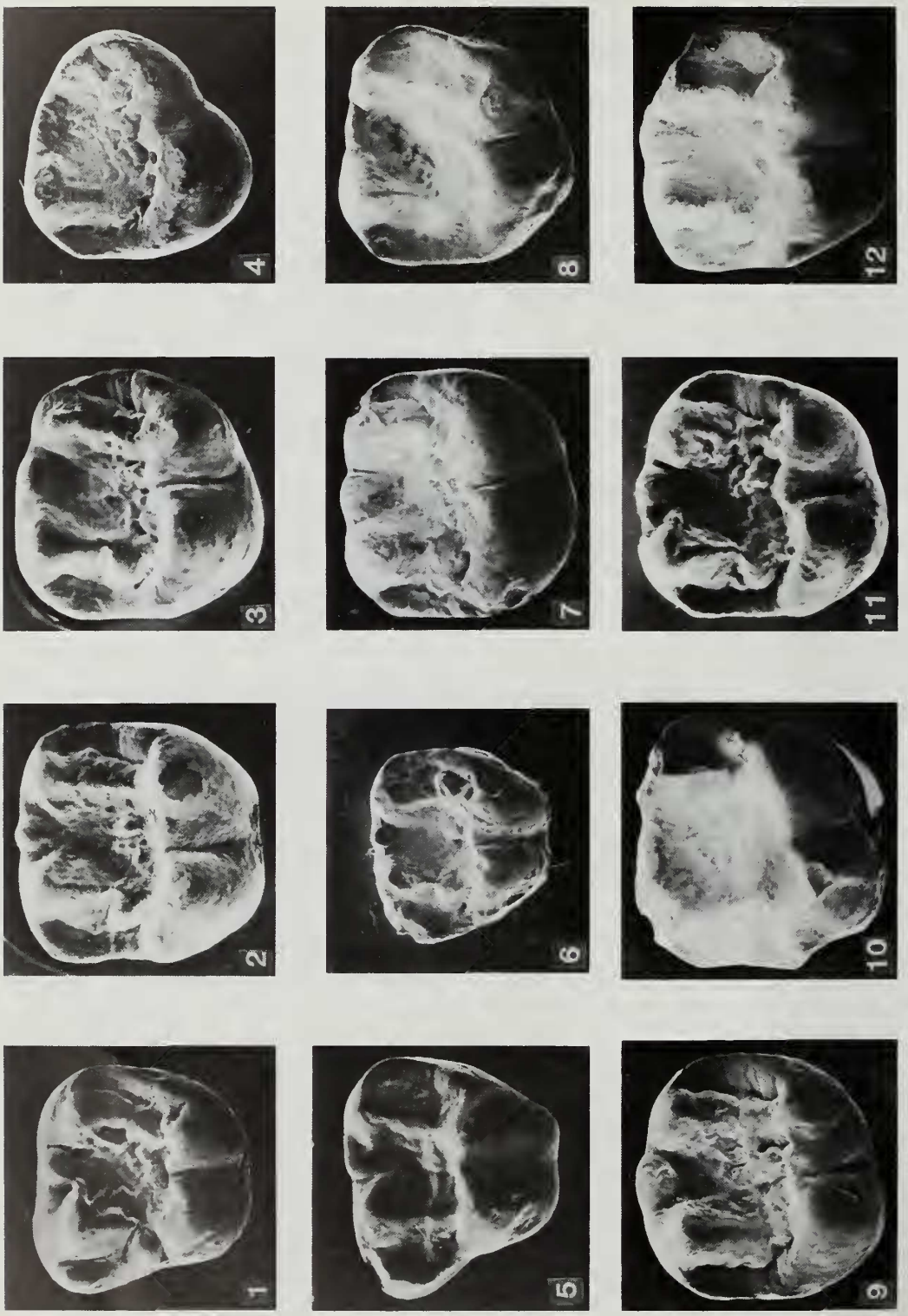
DESCRIPTION. One of the most important discoveries in the Creechbarrow material is of upper and lower fourth permanent premolars. Teeth previously identified as such can now be conclusively identified as upper and lower fourth deciduous premolars. The possibility of DP4 retention in *Suevosciurus* was first suggested by Bosma (1974: 40). She reasoned that no distinction could be made between deciduous and permanent premolars despite the abundant material available and that 'P^4' had a strong parastyle typical of DP^4 in other pseudosciurid genera. The supposed characters of 'P^4' can no longer be used as a constant diagnostic feature for *Suevosciurus* and even though retention of $DP^{\frac{4}{4}}$ characterizes the best-known of the various species, it cannot be used in the generic diagnosis with the inclusion of *S. authodon*. Nevertheless the increase in crown height of $DP^{\frac{4}{4}}$ can be used and this probably foreshadowed later loss of $P^{\frac{4}{4}}$.

There is much variation in practically all the known morphological characters of *Suevosciurus* and size has been used by previous workers almost exclusively to distinguish between species. The low coefficients of variation for the large tooth assemblage from Creechbarrow indicate the presence of a single species (Table 19). An attempt is made here to provide numerical scales for features of variable size (e.g. mesostyle), or just to indicate presence or absence, and to show percentage occurrence within the Creechbarrow assemblage (see Tables 20–21). It is hoped that this will encourage other workers to do the same for their material, to allow species-level distinctions on at least percentage characters. Some are suggested under Phylogenetic Relationships (p. 321).

Table 19 Statistics of length and width measurements of cheek teeth of *Suevosciurus authodon* from Creechbarrow. (Notation as in Table 13, p. 303).

Tooth	Length					Width				
	N	OR	$\bar{x}$	s	v	N	OR	$\bar{x}$	s	v
DP^4	17	1·250–1·550	1·43	0·086	6·00	23	1·150–1·625	1·34	0·099	7·38
P^4	21	1·375–1·625	1·49	0·075	5·06	22	1·350–1·550	1·45	0·066	4·58
$M^{1/2}$	84	1·350–1·625	1·49	0·055	3·71	86	1·375–1·675	1·57	0·068	4·36
M^3	24	1·250–1·500	1·38	0·059	4·25	23	1·325–1·525	1·42	0·053	3·73
DP_4	2	1·350–1·400	1·38	0·035	(2·57)	2	0·975–1·125	1·05	0·106	(10·10)
P_4	12	1·350–1·525	1·44	0·048	3·33	10	1·050–1·250	1·18	0·070	5·89
$M_{1/2}$	88	1·425–1·700	1·57	0·066	4·18	96	1·250–1·500	1·35	0·056	4·17
M_3	42	1·550–1·850	1·70	0·082	4·83	40	1·150–1·500	1·34	0·063	4·72

The specimens figured in Plate 18 show some of the range of variation in $M^{1/2}$s relevant to an understanding of the character developments detailed in Table 20. Metalophule I may be a complete ridge (fig. 8), a lingually restricted ridge (figs 3, 9), reduced to just metaconule 1 (fig. 2) or missing (fig. 7). Size 1 is shown in figs 2–3, size 2 in fig. 9 and size 3 in fig. 12. There may be a minor ridge of enamel joining metaconule 1 to either the endoloph, hypocone, metalophule II or a combination of the three. Fig. 9 shows links to both the endoloph and metalophule II. Metaconule 2 is sometimes present (figs 8, 11) but usually absent (figs 2–3, 7, 9–10, 12). Enamel wrinkling may be fine low beading (fig. 2) or finely (fig. 7) to coarsely (fig. 9) reticulate, and may show degrees of obscuration by wear (figs 8, 12). The sinus may be shallow (fig. 9), of medium depth (fig. 2) or deep (fig. 12); it is nearly always complete. The mesostyle has been given five arbitrary size numbers: 0 (fig. 10), 1 (fig. 8), 2 (fig. 2), 3 (figs 11–12), 4 (figs 3, 7, 9). Its buccal saliency is sometimes but not always related to its size; e.g. there may be an ectoflexus (fig. 10) or the mesostyle may be non-salient (grade 1: fig. 8) or salient in two size grades (2: fig. 3; 3: fig. 9). The mesostyle may be a circular object (fig. 2) or it may be elongated into a partial


1
2
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12

Table 20 Percentage character analysis of upper cheek teeth of *Suevosciurus authodon* from Creechbarrow. For explanation see Table 14.

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Metalophule I shape: metaconule 1 only (1), ridge (2) (10) (0) (18) (30) (0)	1	70		88·9	83·3	
	2	30		11·1	16·7	
Metalophule I size (13) (15) (19) (31) (0)	0	23·1	100	5·3	3·2	
	1	23·1	0	31·6	19·4	
	2	46·1	0	42·1	54·8	
	3	7·7	0	21·0	22·6	
Metalophule I joins endoloph (1), hypocone (2), metalophule II (3), endoloph and hypocone (4), hypocone and metalophule II (5), endoloph and metalophule II (6), all three (7), none (0) (10) (0) (18) (30) (0)	0	10		39·0	13·3	
	1	0		50·0	40·0	
	2	60		5·5	13·3	
	3	30		0	16·8	
	4	0		5·5	0	
	5	0		0	3·3	
	6	0		0	10·0	
	7	0		0	3·3	
Metalophule II broken/unbroken (20) (20) (23) (55) (12)	B	5	25	0	12·7	83·3
	U	95	75	100	87·3	16·7
Enamel wrinkling (0–3) (5) (16) (10) (22) (11)	0	100	0	10	0	0
	1	0	0	60	63·6	0
	2	0	50	30	36·4	45·5
	3	0	50	0	0	54·5
Mesostyle size (0–4) (18) (21) (22) (52) (16)	0	0	0	0	1·9	12·5
	1	11·1	0	9·1	1·9	0
	2	44·4	4·8	9·1	32·8	0
	3	38·9	47·6	59·1	36·5	25·0
	4	5·6	47·6	22·7	26·9	62·5
Mesostyle saliency: prominent (3), slight (2), non (1), ectoflexus (0) (19) (20) (21) (51) (20)	0	26·3	30	4·8	2·0	0
	1	68·4	60	57·1	43·1	40
	2	5·3	10	33·3	35·3	45
	3	0	0	4·8	19·6	15
Mesostyle mesiodistally elongated (19) (21) (22) (52) (21)	0	100	66·7	100	86·5	0
	1	0	33·3	0	13·5	100
Mesoloph length (0–2) (18) (21) (22) (52) (21)	0	5·6	66·7	27·3	44·2	85·7
	1	61·1	23·8	54·5	46·2	14·3
	2	33·3	9·5	18·2	9·6	0

Table 20 (*continued*)

Plate 18 Scanning electron micrographs of upper cheek teeth of *Suevosciurus authodon* sp. nov. from Creechbarrow, × 25. Fig. 1, right P^4 (reversed) (M35795). Fig. 2, left $M^{1/2}$ (M^1?) (M35821). Fig. 3, left $M^{1/2}$ (M^2?) (M35481). Fig. 4, right M^3 (reversed) (M35489). Fig. 5, **holotype** right DP^4 (reversed) (M35469). Fig. 6, left DP^4 (M36447). Fig. 7, right $M^{1/2}$ (M^2?) (reversed) (M35861). Fig. 8, right $M^{1/2}$ (M^2?) (reversed) (M35855). Fig. 9, left $M^{1/2}$ (M^2?) (M35833). Fig. 10, left $M^{1/2}$ (M^2?) (M35838). Fig. 11, right $M^{1/2}$ (reversed) (M35860). Fig. 12, left $M^{1/2}$ (M^2?) (M35844). See p. 315.

Table 20 continued

Characters + (N) of respective teeth	Scoring units	DP^4	P^4	M^1	M^2	M^3
Protolophule 1 broken/unbroken	B	9·5	50	4·4	3·6	23·5
(21) (16) (23) (55) (17)	U	90·5	50	95·6	96·4	76·5
Metaconule 2 absence/presence	0	66·7	65	78·3	62·3	
(21) (20) (23) (53) (0)	1	33·3	35	21·7	37·7	
Hypolophule absent (0), partial	0	85·7	79·0	95·2	70·4	
(1), complete (2)	1	14·3	10·5	4·8	3·7	
(21) (19) (21) (54) (0)	2	0	10·5	0	25·9	
Posteroloph broken/unbroken lingually	B	33·3	36·8	13·0	1·8	
(21) (19) (23) (55) (0)	U	66·7	63·2	87·0	98·2	
Mesocone absence/presence	0	100	100	94·1	91·9	100
(21) (18) (18) (40) (14)	1	0	0	5·9	8·1	0
Sinus depth: shallow (1) to	1	0	0	0	0	4·8
deep (4)	2	5·3	20	4·4	18·2	14·3
(19) (20) (23) (55) (21)	3	68·4	75	52·2	65·5	57·1
	4	26·3	5	43·4	16·3	23·8
Protostyle absence/presence	0	52·9	100	26·3	59·5	75
(17) (18) (19) (37) (16)	1	47·1	0	73·7	40·5	25
Hypostyle absence/presence	0	80·9	73·7	33·3	47·2	
(21) (19) (18) (36) (0)	1	19·1	26·3	66·7	52·8	
Paraconule absent (0), small (1),	0	0	5	0	0	0
large (2)	1	0	5	4·4	5·5	36·8
(21) (20) (23) (55) (19)	2	100	90	95·6	94·5	63·2
Endoloph broken (1), complete (2)	1	0	21·1	4·4	3·6	0
(20) (19) (23) (55) (15)	2	100	78·9	95·6	96·4	100
DP^4 parastyle bicuspid	0	53·3				
(15)	1	46·7				
DP^4 mesiolingual margin concave	0	60				
(20)	1	40				

mesoloph (grade 1: fig. 7; or 2: fig. 12); alternatively it may be mesiodistally elongated (figs 3, 9). Whereas in advanced species of *Suevosciurus* the M^{1-2} paraconule is often reduced, this is so in only four Creechbarrow specimens (e.g. fig. 9). Metalophule II may be broken buccal and/or lingual to the position of metaconule 2 (whether present or absent) and there may be a hypolophule (fig. 7). Other minor cusps which may be present are protostyle (= anterocone), mesocone and hypostyle (fig. 12).

When the usual method of distinguishing M^1 from M^2 (see under Taxonomic Treatment of the Pseudosciuridae, p. 298) was used for this species, it was found that M^2s outnumbered M^1s two to one. One explanation is that the M^2 type morphology commonly occurred in M^1.

On M^3, although the paraconule is often weaker than on M^{1-2}, it may also be accompanied by a crest which joins it to the anteroloph, as on one M^3 of *Sciuroides rissonei* (M36115). Because of the distal tapering of the outline of this tooth, a metacone is present, as shown in Pl. 18, fig. 4, in only three out of twenty specimens.

The $M_{1/2}$s are less variable than the upper molars. The ectolophid/hypolophulid connection

varies from at or very close to the hypoconid (Pl. 17, fig. 8) to about a quarter the distance along the hypolophulid from the hypoconid (fig. 9). The anteroconid is always present and often large; fig. 8 shows a size 1 anteroconid, fig. 9 a size 2 and fig. 12 a size 4. Figs 8–9 show the typical 60–70% filling of the sinusid by the mesoconid. Enamel wrinkling resembles that on M^{1-2}. Most *Suevosciurus* sp. from the Mammal Bed of Hordle Cliff have the buccal end of the mesoconid fused to the hypoconid. Schmidt-Kittler (1971*a*: 44) noted this occasionally also in *S. fraasi* from southern Germany. Proportionately fewer specimens from Creechbarrow than from Hordle have this character.

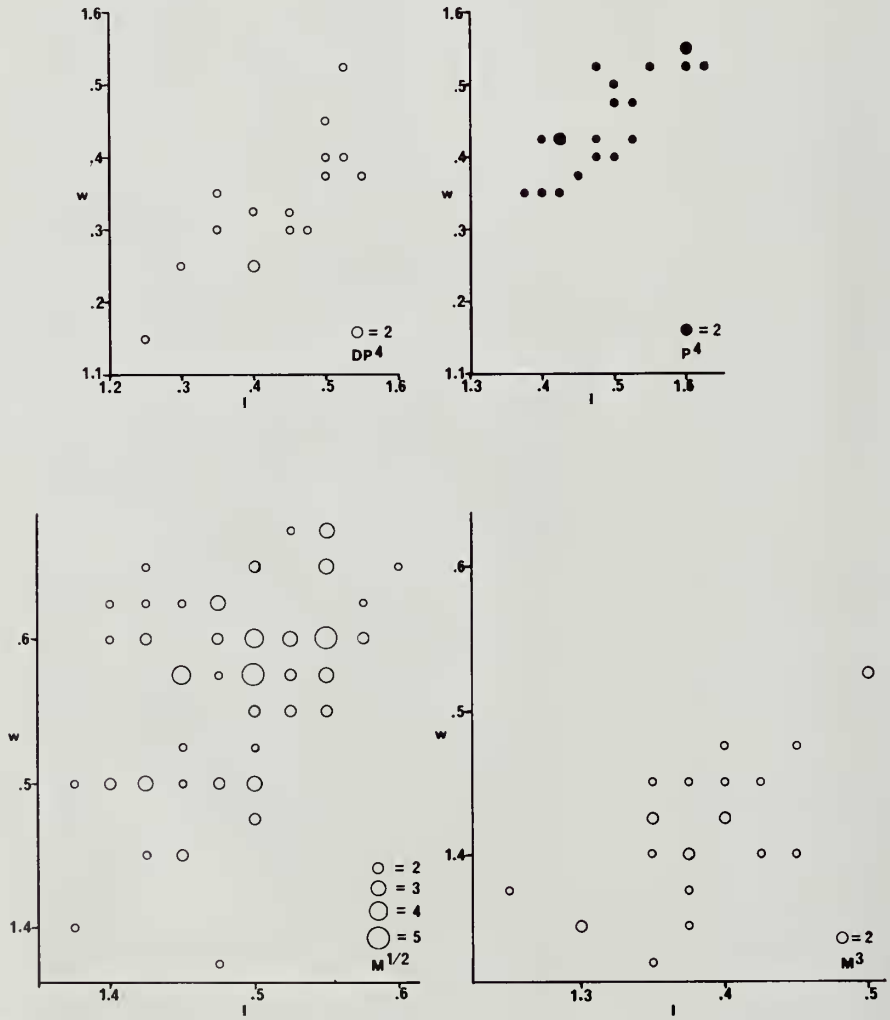
Phylogenetic relationships with other species of *Suevosciurus*. *S. authodon* appears primitive in its retention of $P\frac{4}{4}$; relatively short DP^4; normally large paraconule; normal presence of

Table 21 Percentage character analysis of lower cheek teeth of *Suevosciurus authodon* from Creechbarrow. For explanation see Table 14.

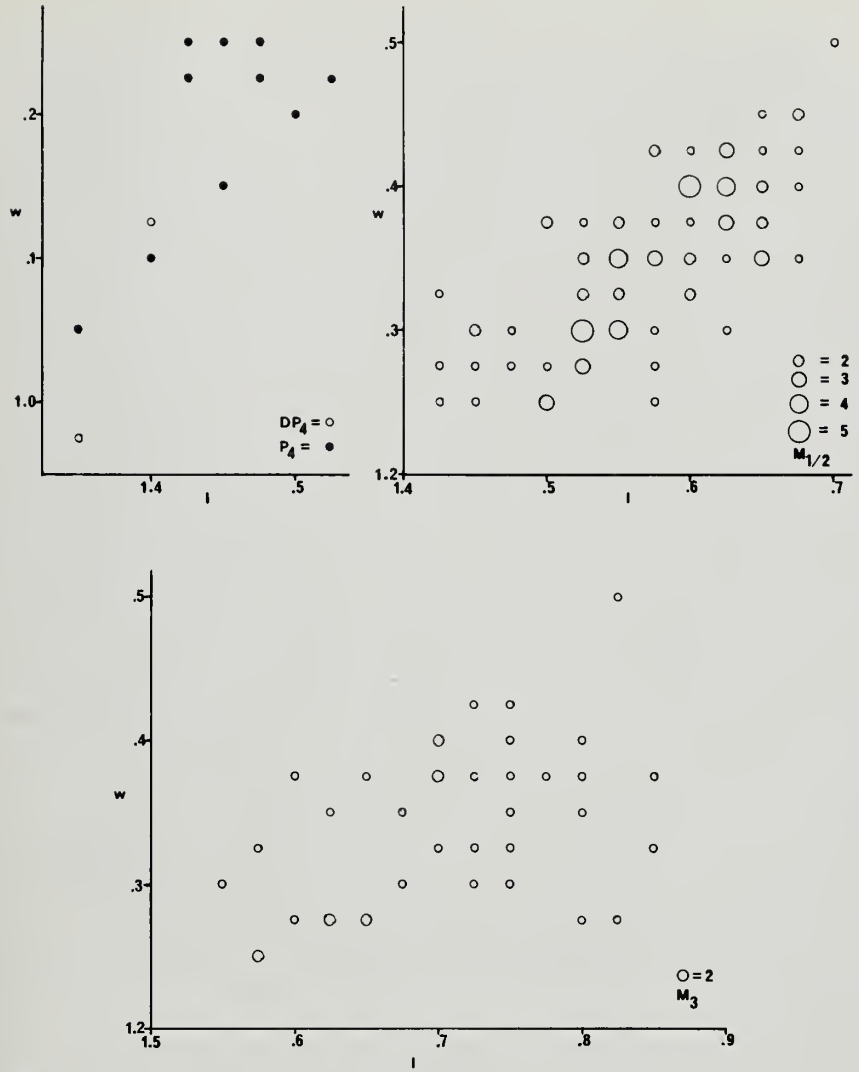
Characters + (N) of respective teeth	Scoring units	DP_4	P_4	M_1	M_2	M_3
Distance along hypolophulid from hypoconid of junction with ectolophid (2) (9) (32) (34) (32)	$<\frac{1}{4}$	50	55·6	78	47	65·6
	$\frac{1}{4}$	50	44·4	22	53	31·3
	no link	0	0	0	0	3·1
Anteroconid size (1–4) (0) (0) (32) (35) (35)	1			3·1	22·9	74·3
	2			21·9	31·4	25·7
	3			59·4	37·1	0
	4			15·6	8·6	0
Anterolophulid absent (0), weak (1) (0) (0) (31) (30) (27)	0			80·7	86·7	40·7
	1			19·3	13·3	59·3
Mesoconid length as % depth of sinusid (2) (9) (31) (36) (33)	50	0	11·1	22·6	27·8	6·1
	60	50	22·2	35·5	19·4	12·1
	70	0	33·4	35·5	27·8	33·3
	80	50	22·2	6·4	13·9	27·3
	90	0	11·1	0	2·8	15·1
	100	0	0	0	8·3	6·1
Mesoconid fused buccally with hypoconid (2) (9) (31) (36) (33)	0	100	100	67·7	78·8	78·8
	1	0	0	32·3	21·2	21·2
Enamel wrinkling (0–3) (2) (6) (23) (18) (21)	0	100	0	8·7	22·2	0
	1	0	0	73·9	50·0	14·2
	2	0	50	17·4	27·8	42·9
	3	0	50	0	0	42·9
Mesostylid absence/presence (2) (9) (33) (38) (26)	0	100	100	93·9	100	70
	1	0	0	6·1	0	30
Ectostylid absence/presence (2) (9) (32) (37) (33)	0	100	100	96·9	83·8	100
	1	0	0	3·1	16·2	0
Hypoconulid absence/presence (2) (9) (33) (32) (30)	0	100	44·4	51·5	71·9	86·7
	1	0	55·6	48·5	28·1	13·3
Distal crest to hypolophulid absence/presence (2) (9) (34) (35) (26)	0	100	77·8	97·1	85·7	96·1
	1	0	22·2	2·9	14·3	3·9

incomplete metalophule I with large metaconule 1; and normally complete M_3 hypolophulid. In all other assemblages of *Suevosciurus* species where cheek teeth mesial to the molars are known, only $DP\frac{4}{4}$ (never $P\frac{4}{4}$) have been found; this tooth tends to have a higher length/width ratio than in *S. authodon* (except in the holotype of *S. ehingensis*), although there is some overlap. In assemblages from the early Ludian of the Isle of Wight a short incomplete metalophule I is occasionally present (Bosma 1974: 40); it also occurs in the Bavarian assemblages (Schmidt-Kittler 1971*a*: text-fig. 17). In assemblages of *Suevosciurus* other than from Creechbarrow, the $M^{1/2}$ metaconule 2 is normally missing. It is not mentioned by Bosma (1974) as occurring in the Isle of Wight assemblages and only occasionally as a vestigial feature by Schmidt-Kittler (1971*a*: 40, text-fig. 17a).

Attempts to compare the Creechbarrow *Suevosciurus* with existing material from the literature are hampered by the lack of numerically delineated information on morphological variation and the belief that the various species only differ in size.



Text-figure 36 Scatter diagrams of length (l) against width (w) in DP^4, P^4, $M^{1/2}$ and M^3 of *Suevosciurus authodon* sp. nov. from Creechbarrow. Measurements in millimetres.



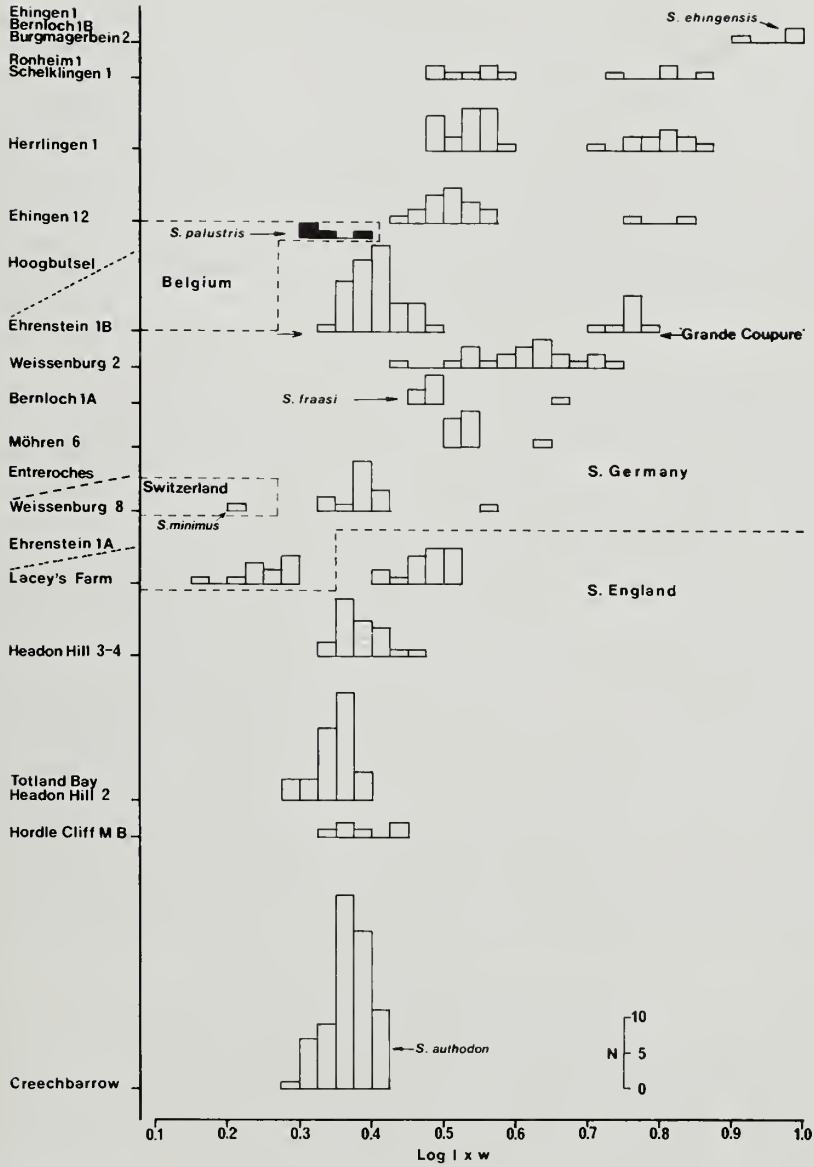
Text-figure 37 Scatter diagrams of length (l) against width (w) in DP_4, P_4, $M_{1/2}$ and M_3 of *Suevosciurus authodon* sp. nov. from Creechbarrow. Measurements in millimetres.

Schmidt-Kittler (1971*a*) identified two principal lineages of *Suevosciurus* which differed in size where found together at any one locality. The sequence of fissure-fill localities he dated by correlating other elements of their mammal faunas with those known from stratified sequences elsewhere in Europe. The smaller lineage he referred to *S. fraasi*, the larger to *S. ehingensis*. Each lineage fluctuated in size somewhat but there was a net size increase with time. Some very small teeth from Ehrenstein 1A and Weissenburg 6 he removed from his two lineages and identified as *S. minimus* on the basis of size. Bosma (1974) also demonstrated a slight size increase in a sequence of three superposed horizons in the Isle of Wight Ludian. She noted the problem of identification posed by those of Schmidt-Kittler's assemblages with only one species of *Suevosciurus*, as there is overlap if all assemblages are considered together. To avoid identifying them by horizon determined in turn by the associated fauna, she suggested a classification based on arbitrary size groupings. The result was the identification of parts of the *S. ehingensis*

lineage as *S. fraasi* and parts of the *S. fraasi* lineage as *S. palustris*. In addition, she calculated that there was an undescribed species intermediate in size between *S. fraasi* and *S. ehingensis*. On the same basis, material from the Headon Beds was identified as *S. palustris* and that from the Osborne Beds (Bosma & Insole 1976) as *S. fraasi*.

Two different displays of the published data plus some new data are presented here in an attempt to test the credibility of the lineages and also to search for ways of identifying species other than by purely single parameters or by stratigraphy. Firstly (Text-fig. 38) histograms of the log of length × width of $M^{1/2}$ have been plotted in stratigraphical order. The record is not as dense as it is for part of the Wyoming early Eocene (see Gingerich 1976*a*) and more than one phylogenetic interpretation is possible. After the Grande Coupure most of the Bavarian localities contain a larger and a smaller species which show only a slight size increase with time. Of these the smaller one can readily be identified with *S. fraasi* on size. The larger, however, is considerably smaller than the type assemblage of *S. ehingensis* from the later (Antoingt Zone) Ehingen 1 locality. Where two species are present in Bavarian fissure fillings prior to the Grande Coupure, there is more size variation between localities and consequent overlap in total. Moreover, the smaller species is in most cases the more abundant, except in the last locality prior to the Grande Coupure (Weissenburg 2) where the larger has a wide observed range into which the one smaller specimen (doubtfully attributed by Schmidt-Kittler to *S. fraasi*) could possibly be incorporated. If the two post-Grand Coupure lineages could be shown to be derived from this single variable species, then the smaller one could no longer be identified as *S. fraasi*, whose type locality is slightly older. On the other hand, the Weissenburg 2 histogram is bimodal and the length measurements produce a coefficient of variation of 9·11, twice that of the unimodal assemblages with at least twenty specimens. It appears thus that two species are represented in the Weissenburg 2 assemblage, but more than just the smallest specimen should be referred to *S. fraasi* (see Schmidt-Kittler 1971*a*: 109). Overlap of measurements, however, means that it is impossible to identify all specimens. If more specimens from earlier pre-Grande Coupure Bavarian sites were known, they would probably overlap like those of Weissenburg 2. Nevertheless, the presence of the same two lineages from Weissenburg 8 until Ronheim 1 is supported by the length × width histograms.

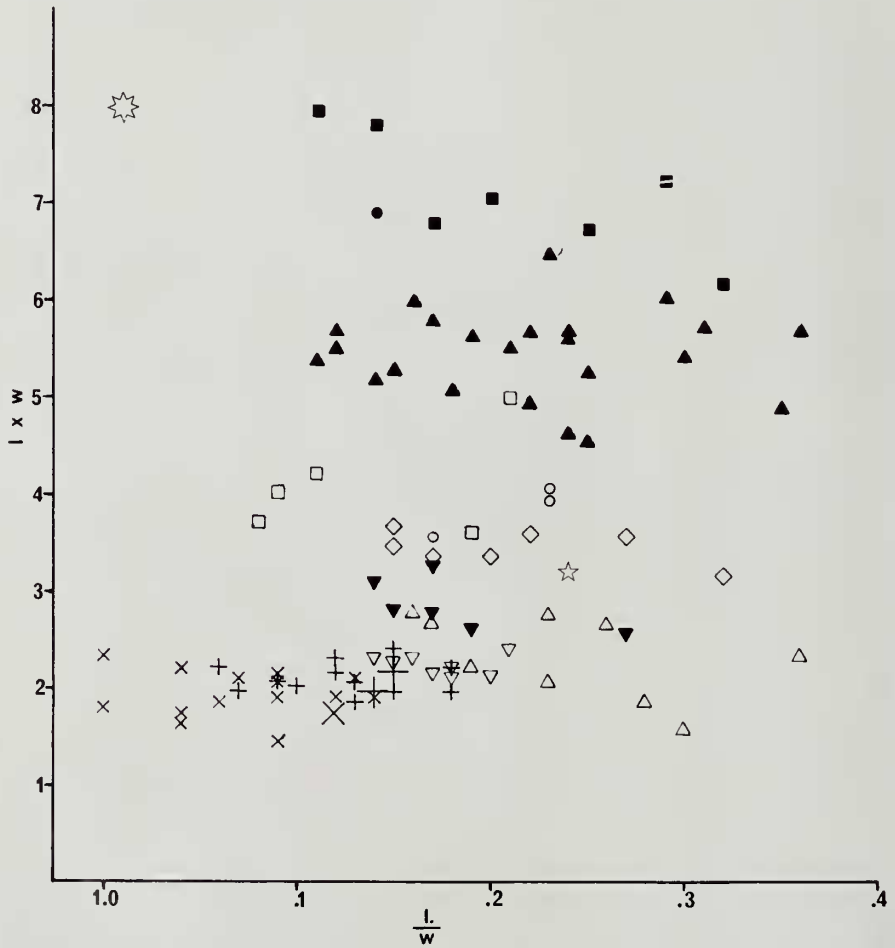
Turning now to the Isle of Wight assemblages, those from the Headon Beds were identified by Bosma (1974) as *S. palustris*. She nevertheless noted that on the single upper molar of this species in the GIU from the type locality, the mesostyle was hardly developed. The holotype and three topotype $M^{1/2}$s in the IRSNB, now cleaned of wax, show a similar poor development of the mesostyle; so does GIU HB801. Schmidt-Kittler (1971*a*: 40) mentioned the presence of well-developed mesostyles in his assemblages and Bosma (1974: 40) noted that although variable the mesostyle was usually relatively high in her assemblages. Out of 74 $M^{1/2}$s from Creechbarrow, only 3 have mesostyles as poorly developed as those of *S. palustris*. Specimens from the Osborne Beds of Lacey's Farm Quarry, Isle of Wight, were identified by Bosma & Insole (1976) as *S. fraasi* on the basis of size. They are intermediate between the larger and smaller species present at Weissenburg 8, a locality probably only slightly younger than Lacey's Farm Quarry. They overlap with the smaller species and probably would also overlap with the larger species if more specimens were known. The Lacey's Farm Quarry assemblage appears a good candidate for potential common ancestry of both the larger and smaller lineages. Alternatively, *S. minimus* from Ehrenstein 1A could have given rise to the smaller species and the Lacey's Farm Quarry assemblage to the larger species. Unfortunately little is known of *S. minimus* from any locality so that assessment of its position in the phylogeny is not yet possible. Either of the two above alternatives appear more plausible in the light of the Isle of Wight material, however, than Schmidt-Kittler's (1971*a*: 119) idea that *S. minimus* was the common ancestor of both lineages. The placing of *S. minimus* in an ancestral position probably arose because he thought the holotype came from the Bartonian fissure of Eclépens-Gare. However, a label with the specimen in the LGM in Stehlin's writing gives 'Entreroches', which is a later Ludian fissure. That this is the correct provenance is supported by the record of 'une très petite mandibule inférieure portant quatre molaires et une incisive' belonging to a 'Rongeur' by Harpe & Gaudin (1854: 127).



Text-figure 38 Histograms of log. length × width in stratigraphic order of $M^{1/2}$ of species of *Suevosciurus* from localities in England, Switzerland, southern Germany and Belgium, spanning Bartonian to Stampian. For measurements and references to localities see Cray (1973), Bosma (1974), Bosma & Insole (1976), Insole (1972) and herein for England, Stehlin (1903) for Switzerland, Schmidt-Kittler (1971*a*) for southern Germany and Misonne (1957) for Belgium. The histogram of *S. palustris* (Misonne) is shown solid to indicate that it is morphologically separable from its contemporary *S. fraasi* Major from Ehrenstein 1B. The single plot of *S. minimus* (Major) from Entreroches is estimated from the unique M_1, by squaring its length. Names of species arrowed indicate type assemblages or age of type assemblage (*S. fraasi*).

The second combination of parameters is shown in Text-fig. 39. It plots length × width against length/width of DP^4. The lowest length/width ratio is shared by the Creechbarrow species and the holotype of *S. ehingensis*, which can be distinguished easily on absolute size. The larger species from Ehrenstein 1B, Herrlingen 1 and Schelklingen 1 have higher ratios. The smaller species from Bernloch 1A, Ehrenstein 1B, Ehingen 12, Herrlingen 1, Schelklingen 1 and Ronheim 1 in total spans the ratio of the larger species but is less variable (possibly an artifact of lower numbers) in each locality; in the smaller species the assemblages with the smaller teeth have a higher length/width ratio than those with the larger teeth.

Specimens from Lacey's Farm Quarry fit easily within the range of *S. fraasi*. However, as no pre-Grande Coupure DP^4s belonging to the larger Bavarian species are known, no concomitant contrast can be made. The teeth from the Headon Beds are similar in size to the smallest in the smaller Bavarian lineage from Ehrenstein 1B. Both were identified by Bosma as *S. palustris*.



Text-figure 39 Scatter diagram of length × width against length/width in DP^4 of species of *Suevosciurus*. Key: × = Creechbarrow; + = HH2 and TB; ▽ = HH3–4; ▼ = Lacey's Farm Quarry; ☆ = *S. fraasi* Major from Bernloch 1A; △ = *S. fraasi* from Ehrenstein 1B; ▲ = the larger lineage from Ehrenstein 1B; ◇ = *S. fraasi* from Ehingen 12; □ = *S. fraasi* from Herrlingen 1; ■ = the larger lineage from Herrlingen 1; ○ = *S. fraasi* from Ronheim 1 and Schelklingen 1; ● = the larger lineage from Schelklingen 1; and ☆ = *S. ehingensis* Dehm from Ehingen 1. For data sources see Text-fig. 38, p. 325.

The Headon Beds teeth can be distinguished by their length/width ratios, which are intermediate between those from Ehrenstein 1B and those from Creechbarrow, slightly overlapping both. Their stratigraphical trend is towards higher length/width ratio. In the light of the few Hordle Cliff specimens and the histograms shown here, Bosma's (1974) claimed size increase through the Headon Beds does not appear to be a significant trend. On the basis of mesostyle size, neither the Headon Beds *Suevosciurus* nor the smallest members of the smaller Bavarian lineage deserves to be identified as *S. palustris*.

Can *Suevosciurus authodon* be considered the common ancestor for all later species of the genus? It *is* the oldest and most primitive known. No assemblages with two species are known until Ehrenstein 1A. Without a better Bartonian record, it is not possible to judge whether or not *S. authodon* was actually the common ancestral species for *Suevosciurus*, but it nevertheless represents a good morphological ancestor. The absence of any authenticated records of *Suevosciurus* from non-British Bartonian sites suggests that it may have originated in the area of southern England and later spread to the rest of Europe.

Relationship with *Treposciurus*. Although *Suevosciurus authodon* has many of the characters of later *Suevosciurus* species, these are often less developed or occur in a smaller percentage of individuals in the assemblage. Moreover, its ability to replace DP^4_4 with P^4_4 and the characters of this latter tooth closely resemble *Treposciurus helveticus preecei*. Close relationship is indicated and it is likely that they had a very recent common ancestry within the Bartonian.

Recommendations on application of current specific names. 1. *S. ehingensis* should be restricted to material from Ehingen 1, Bernloch 1B and Burgmagerbein 2, comprising very large teeth and a DP^4 with a length/width ratio of about 1.

2. *S. palustris* should be restricted to the small teeth from Hoogbutsel with upper molar mesostyles minute or missing.

3. *S. fraasi* should be used for the smaller of the two main Bavarian lineages, characterized by having DP^4 with a very prominent parastyle.

4. *S. minimus* should be used for the holotype M_{1-3} from Entreroches, about which more information is needed before its status can be assessed, and the isolated molars from Ehrenstein 1A and Weissenburg 6.

This leaves, as two definable unnamed species, members of the main larger Bavarian lineage (referred by Schmidt-Kittler 1971*a* to *S. ehingensis*) and the small teeth from the Headon Beds (referred by Bosma 1974 to *S. palustris*). More problematical are the teeth from Lacey's Farm Quarry. More material from critical levels and in more geographical areas would improve our knowledge of the interrelationships within this complex genus, whose biostratigraphical potential is high.

Order **APATOTHERIA** Scott & Jepsen 1936

I follow Sigé (1975) and Russell *et al.* (1979) in recognizing this group as a distinct order. Its position herein adjacent to the Carnivora and distant from the Proteutheria reflects its relationships with the palaeoryctids as advocated by Szalay (1968), themselves showing specializations towards creodonts, carnivores and condylarths (see Van Valen, 1966). It comprises only one family unless *Aethomylos* Novacek 1976 is an apatothere (see Novacek, 1976: 40–44, figs 16–19).

Family **APATEMYIDAE** Matthew 1909

Type genus. *Apatemys* Marsh 1872.

Included genera. *Jepsenella* Simpson 1940; *Labidolemur* Matthew & Granger 1921; *Stehlinella* Matthew 1929*c*; *Sinclairella* Jepsen 1934; *Eochiromys* Teilhard 1927; *Heterohyus* Gervais 1852.

Range. Middle Palaeocene–Oligocene, North America; late Palaeocene–late Eocene, Europe.

Diagnosis. See McKenna (1963: 13).

Table 22 Distribution of characters (except size) in the different post-Ypresian species of *Heterohyus*. As *H. heufelderi* and *H. gracilis* appear identical in all characters except the relative sizes of P_3 and P_4 based on alveoli, characters virtually unknown for the other species, they are considered together. Characters are estimated as primitive (−) or advanced (+) based on outgroup comparison with the rest of the Apatemyidae. Characters 1 to 12 involve upper molars; characters 13 to 25 involve lower molars. Lack of information on a character is indicated by '?'.

Character	State: primitive	State: advanced	*H. armatus*	*H. europaeus*	*H. gracilis* and *H. heufelderi*	*H. sudrei*	*H.* sp., Malpérié	*H. nanus*	*H. morinionensis*	*H. quercyi*
1 M^1 parastyle strength	weak	strong	?	−	?	+	?	+	?	+
2 M^2 buccally salient parastyle	yes	no	?	?	−	?	+	−	+	+
3 M^2 ditto strength	strong	weak	?	?	+	?		−		
4 M^2 parastyle mesially salient	yes	no	?	?	+	?	+	+	−	−
5 M^2 ectoflexus	shallow	deep	?	?	+	+	−	+	−	−
6 M^{1-2} postmetacrista	present	absent	?	+	−	−	−	−	−	−
7 M^{1-2} postmetacrista strength	weak	strong	?		−	+	−	−	−	−
8 M hypocone	small	large	?	−	−	−	−	−	+	+
9 M postprotocingulum joining hypocone	no	yes	?	−	−	+	−	−	−	−
10 M postprotocrista	yes	no	?	+	−	+	+	+	−	−
11 M postprotocrista strength	weak	strong	?		−				−	+
12 M posthypocrista	weak	strong	?	−	+	+	+	−	−	−
13 M_2 lingual hypoconulid	no	yes	−	+	−	−	?	−	−	?
14 M_{1-2} entoconid notch	no	yes	−	−	+	+	?	−	−	?
15 M talonid length	short	long	−	−	+	+	?	−	−	−
16 M trigonid length	long	short	−	+	−	−	?	+	+	+
17 M entoconid	weak	strong	+	+	−	−	?	+	+	+?
18 M paraconid	weak	strong	+?	+	−	+	?	−	−	+
19 M mesial paracristid limb	absent	present	+	+	−	−	?	−	−	+
20 M ditto strength	weak	strong	+	−			?			+
21 M postcristid	transverse	oblique	+	−	+	+	?	−	−	−
22 $M_3 : M_2$ length ratio	low	high	−/+	−	−	?	?	+	−	+
23 M_3 hypoconulid cusp length	short	long	−	−	−	?	?	−	−	+
24 M_3 hypoconulid lobe extending talonid	no	yes	−/+	−	−	?	?	+	−	−
25 M_3 hypoconulid bulging buccally	no	yes	−/+	−	−	?	?	−	+	−
26 Lower incisor	narrow	wide	−	+	−	?	?	−	?	−
27 Depth of mandible	shallow	deep	−	+	−	?	?	−	?	−
28 Ascending ramus	behind M_3	beside M_3	−	+	−	?	?	−	?	−

Genus *HETEROHYUS* Gervais 1852

[incl. *Necrosorex* Filhol 1890*c*, *Amphichiromys* and *Heterochiromys* Stehlin 1916, *Heterohyus* (*Chardinyus*) and *H.* (*Gardonyus*) Sigé 1975]

TYPE SPECIES. *H. armatus* Gervais 1852. Middle Lutetian, Bouxwiller, France.

INCLUDED SPECIES. *H. europaeus* (Stehlin 1916) Teilhard 1922; *H. gracilis* (Stehlin 1916) Teilhard 1922; *H. heufelderi* Heller 1930 (doubtfully distinct from *H. gracilis*, but see discussion in Russell *et al.*, 1979: 226); *H. sudrei* Sigé 1975; *H. quercyi* (Filhol 1890*c*) Teilhard 1922; *H. nanus* Teilhard 1922; *H. morinionensis* sp. nov.; *H.* sp. from Malpérié and La Bouffie (see Sigé 1975: 665); *H.* sp. from Hordle Cliff (see Cray 1973: 63–64); *H.* sp. from Mutigny; *H.* spp. 1, 2, 3 from Avenay; *H.* spp. [1, 2] from Grauves and Cuis (see Russell *et al.*, 1979: 227–231).

RANGE. Ypresian–Ludian, France; late Lutetian, Switzerland; early Lutetian, D.D.R.; Marinesian–early Ludian, England.

DIAGNOSIS. See Sigé (1975: 656) for the most recent formal diagnosis; but see Russell *et al.* (1979: 222–226) for comprehensive discussion of generic characters.

DISCUSSION. Species of this genus, like the others in the Apatemyidae, are rare faunal elements and are known mainly from scattered, isolated teeth. A few jaws are known but the only specimen with upper and lower teeth associated (referred specimen of *H. quercyi*) is lost (*fide* Sigé 1975: 658). There are thus often problems in associating both different tooth types in a single row and uppers and lowers of the same species. Occlusal studies have not been published.

Table 22 shows the distribution of characters in the different post-Ypresian species (named and unnamed). Various attempts have been made in the past to divide the genus *Heterohyus* into different genera or subgenera (see synonymy list above, Sigé 1975 and Russell *et al.* 1979). The table shows that most of the available characters have a rather random distribution with few congruencies. The position is further complicated by the incompleteness of different taxa and the consequent poor overlap of parts known.

Small numbers of specimens restrict the knowledge of intraspecific variation. However, some such variation can be seen in Table 22 in characters 22, 24, and 25.

Neither a phenetic comparison, using all the characters, nor a cladistic one using only advanced characters (giving shared character states as percentages of the shared characters in both cases) give reliable results (see Table 23). The only exceptions are the very high dissimi-

Table 23 Number of character states in common between the different species of *Heterohyus*. Numbers are percentages of the total characters shared. Above the oblique line only advanced character states are used; below it all the character states are used. Characters are from Table 22.

	H. armatus	*H. europaeus*	*H. gracilis* and *H. heufelderi*	*H. sudrei*	*H.* sp., Malpérié	*H. nanus*	*H. morinionensis*	*H. quercyi*
H. armatus		19	7	25	–	20	17	36
H. europaeus	56		0	14	20	14	12	20
H. gracilis and *H. heufelderi*	67	30		33	40	8	0	0
H. sudrei	50	21	73		29	20	0	14
H. sp., Malpérié	–	60	67	57		22	11	11
H. nanus	73	57	60	47	67		10	17
H. morinionensis	58	59	50	20	56	62		20
H. quercyi	79	50	39	21	56	57	70	

larities of *H. gracilis/heufelderi* from *H. europaeus* and *H. quercyi* and of *H. morinionensis* from *H. gracilis/heufelderi* and *H. sudrei*. The only high similarities are *H. quercyi* with *H. armatus* and the *H.* sp. from Malpérié with *H. gracilis/heufelderi*, both artificially increased by the reduced number of shared anatomical parts known: *H. armatus* is only known from lower teeth, *H.* sp. from Malpérié only from one M^2. A further complication is that the upper dentition attributed to *H. quercyi* may not belong to this species. Future collecting in Europe may well allow more characters to be added for different species, thus helping to clarify relationships.

Heterohyus cf. *sudrei* Sigé 1975
(Pl. 19, fig. 7; Text-fig. 40E; Tables 22, 23)

HOLOTYPE of *H. sudrei*. Left M^3 (UM RBN5170). Lower Calcaire de Fons (Marinesian), Robiac-Nord, France.

RANGE of *H. sudrei*. Marinesian to early Ludian, France.

DIAGNOSIS of *H. sudrei*. See Sigé (1975: 657).

MATERIAL. Left $M_{1/2}$ talonid fragment (M35707).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. This specimen cannot be included in the best represented species from Creechbarrow (*H. morinionensis*) as it is slightly smaller; it has an entoconid notch, a slightly lower entoconid, and the buccal hypoconid wall is more vertical, meeting the postcristid at an acute angle when viewed distally. This compares well with *H. sudrei* (see Text-fig. 40E–F). In *H. morinionensis* and *H. nanus* the angle is 90° or more (Text-fig. 40A–D).

The rather longitudinal orientation of the cristid obliqua and its apparent buccal position of attachment to the trigonid suggests that the tooth is more likely to be an M_1 than an M_2. It has a large distal interstitial facet. Wear on the crown is slight. Just lingual of the midpoint of the postcristid on the mesial side is the faint swelling of a hypoconulid. There is a well-marked valley between this and the entoconid. Because of lingual breakage no width measurement is possible. However, it is slightly smaller than the M_2s of *H. sudrei* figured by Sigé (1975: pl. 2, figs 1–2).

Heterohyus aff. *nanus* Teilhard 1922
(Pl. 19, fig. 6; Text-fig. 40C; Table 24)

v. *1980 Heterohyus* sp. 2; Hooker & Insole: 40.

HOLOTYPE of *H. nanus*. Left mandibular ramus with incisor, P_4, M_{2-3} (MNHN Qu8732). Phosphorites, Mémerlein, France.

RANGE of *H. nanus*. Marinesian to Ludian, France.

DIAGNOSIS of *H. nanus*. See Sigé (1975: 659).

MATERIAL. Left M_2 (M35709).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION AND DISCUSSION. The tooth is unworn but broken distolingually so that the entoconid is now missing. The angle that the postcristid makes with the buccal hypoconid wall, however, is obtuse, suggesting that the entoconid was developed as in *H. nanus* (i.e. larger than in *H. sudrei*). There is a small paraconid and the trigonid is open mesially, the mesial limb of the paracristid being absent, its place being taken by a mesial cingulum. Both trigonid and talonid are relatively short and the whole tooth is thus not much longer than wide.

All these characters suggest strong affinities with *H. nanus*. It is, however, smaller (Table 24), being closer in size to M_2 of *H.* sp. from Malpérié and La Bouffie (Sigé 1975: 665; pl. 1, figs 14–15). There appears to be a slight size increase with time for M^1, M^2 and M_2 from the

Table 24 Length (l) and trigonid (w_1) and talonid (w_2) width measurements of teeth of *Heterohyus* from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1		w_2
H. morinionensis:					
M35702	M^1	–		2·65	
M35703	M^2	2·85		–	
M35400	M^3	2·35		(3·50)	
M35705	M_2	2·40	2·00		1·95
M35706	M_3	–	–		1·90
H. aff. *nanus*:					
M35709	M_2	1·70	1·50		–

Robiac assemblage to those of Malpérié and Perrière (Sigé 1975: text-fig. 3); the Creechbarrow tooth might represent an earlier stage in this trend, but this can only be corroborated by the finding of more teeth and tooth types.

Heterohyus morinionensis sp. nov.
(Pl. 19, figs 1–5; Text-fig. 40D; Tables 22–24)

v. *1977b Heterohyus* (*Chardinyus*) sp.; Hooker: 141.
v. *1980 Heterohyus* sp. 1; Hooker & Insole: 40.

Name. Morinio, a Roman station in the present borough of Wareham, near Creechbarrow.

Holotype. Left M^3, M35400. Pl. 19, fig. 3.

Paratypes. Left M^1 (M35702); right M^2 (M35703); right M^3 (M37119); lingual fragment of left M^3 (M35704); right M_2 (M35705); left M_3 talonid fragment (M35706).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Diagnosis. Medium–small species of *Heterohyus* (M^2 length 2·85 mm; see Table 24). M^2 with parastyle mesially but not buccally salient, and ectoflexus shallow. M^{1-2} with weak postmetacrista. Upper molars with large, well differentiated hypocone with weak posthypocrista and weak postprotocrista. M_2 without hypoconulid. M_{1-2} without entoconid notch. Lower molars with short trigonid and talonid; strong entoconid; weak paraconid; no mesial paracristid limb; and transverse postcristid. M_3/M_2 length ratio low. M_3 with short hypoconulid on short hypoconulid lobe, bulging buccally.

Description. M^1: The postprotocingulum is weak and the large, lingually salient hypocone is separated from it by a notch (Pl. 19, fig. 1). The parastyle and metastyle are broken away but the ectoflexus appears to have been at best very shallow. There is very weak postflexus. The distal cingulum peters out lingually but a continuation down the distal side of the hypocone takes the form of faint papillae.

M^2: This tooth is broken lingually and has a deep postflexus (Pl. 19, fig. 2). The metacone is formed lingually into a strong ridge confluent with the postprotocrista. There is a moderate ectoflexus.

M^3: On the holotype the parastyle is broken at its tip but when complete would have been very prominent buccally (Pl. 19, fig. 3). The postprotocrista appears very weak but may have been largely removed by wear. The two other fragmentary specimens show a constancy for the distinctness of the hypocone from the protocone, although the hypocone is slightly smaller in M35704 than in the other two specimens. M37119 is less worn than the holotype but shows the postprotocrista to be absent, a sharp even valley linking the trigon and talon basins.

M_2: The paraconid is broken away and the edge of the talonid notch, metaconid and entoconid slightly chipped (Pl. 19, fig. 4). Otherwise the tooth is well preserved, moderately

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2

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5

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8a

8b

8c

9

worn with well-defined wear facets. The entoconid is distally positioned, confluent with the postcristid and there is no hypoconulid. A weak lingual rib on the protoconid half crosses the trigonid basin. There is a weak mesial cingulum but no mesial paracristid arm, so that the trigonid basin is open mesially.

M_3: This talonid fragment is truncated through the talonid notch and just behind the tip of the hypoconid (Pl. 19, fig. 5). Its most distinctive feature is the short buccal hypoconulid lobe. The hypoconulid appears to project buccally slightly beyond the hypoconid. The hypoconulid is like that in *H. quercyi* in one respect, that it is slightly constricted, unlike *H. nanus* where it merges imperceptibly in occlusal view with the rest of the talonid. Shape of the talonid appears to be variable (see discussion below).

Discussion. When all characters are considered (including size), *H. morinionensis* is most similar to *H. quercyi*. This is, however, reliant on the correct attribution of the lost cranium and mandible figured by Teilhard (1922: text-fig. 39; pl. 4, figs 16–18). One must therefore first consider the likelihood of the specific association of this specimen with the holotype mandible with M_3.

In all the sufficiently known species of *Heterohyus* except *H. nanus* and *H. quercyi* there is a correlation between the upper molar postprotocrista and the lower molar paraconid. If the former is present the latter is weak; if the former is absent, the latter is strong. In *H. nanus*, lower molars with weak paraconids are 'associated' with upper molars without postprotocristae. In *H. quercyi*, M_3 with a strong paraconid is apparently associated with upper molars with postprotocristae.

Sigé (1975: pl. 1, figs 6–7) figured an M^1 and M^2 from Aubrelong 2 which he considered close in size and morphology to *H. quercyi*, but which he placed with some doubt in *H. sudrei*. His first identification as *H. quercyi*? is tentatively accepted here. These teeth are very similar to those of *H. morinionensis*, differing only in being slightly larger, having slightly stronger postprotocristae and shallower ectoflexus in M^2.

H. morinionensis upper molars occur at Creechbarrow with three different types of lower molars. Two of these have already been identified as *H.* cf. *sudrei* and *H.* aff. *nanus*, both being smaller than the third type, which are of appropriate size for the *H. morinionensis* upper molars. Furthermore, the M_2 of the third type (M35705) has a deeply grooved oblique buccal phase facet on the distal hypoconid wall (see Text-fig. 40D), which is considerably stronger and more oblique than the same facet on otherwise similar lower molars of *H. nanus*. It is most likely to have been caused by an M^2 metacone strengthened by the buccal end of a postprotocrista. Although the trigonid of M_3 is unknown in *H. morinionensis*, judged from a mandibular ramus of *H. nanus* (Sigé 1975: pl. 2, fig. 8a–c) the paraconid alters little in strength from M_1 to M_3. The M_3 paraconid in *H. morinionensis* is thus likely to have been considerably smaller than that of the holotype of *H. quercyi*.

The quality of Teilhard's (1922) retouched photographs of the referred cranium and mandible of *H. quercyi* is poor and the exact details of the teeth are confusing, the different scale photographs being partly contradictory. The lower teeth are mainly obscured, but M_1 (his pl. 4, fig. 17) does appear to have a strong paraconid, thus supporting his identification. It is possible

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Plate 19 Teeth of *Heterohyus* and *Lophiotherium* from Creechbarrow.

Figs 1–5 *Heterohyus morinionensis* sp. nov. Scanning electron micrographs of occlusal views of molars, × 16. Fig. 1, left M^1 (M35702). Fig. 2, right M^2 (reversed) (M35703). Fig. 3, **holotype** left M^3 (M35400). Fig. 4, right M_2 (reversed) (M35705). Fig. 5, left M_3 talonid fragment (M35706). See p. 331.

Fig. 6 *Heterohyus* aff. *nanus* Teilhard. Scanning electron micrograph of occlusal view of left M_2, × 16 (M35709). See p. 330.

Fig. 7 *Heterohyus* cf. *sudrei* Sigé. Scanning electron micrograph of occlusal view of left $M_{1/2}$ talonid fragment, × 16 (M35707). See p. 330.

Figs 8–9 *Lophiotherium siderolithicum* (Pictet). Light macrographs of lower teeth, × 3. Fig. 8a–c, associated left P_4, M_{2-3}; a, buccal, b, occlusal and c, lingual views (M37705). Fig. 9, lingual view of right lower canine (reversed) (M36828). See p. 347.

that the strengthening of the lower molar paraconid plus paracristid is a trend, independent of that occurring earlier in *H. armatus* and *H. europaeus*, and associated with similar strengthening of the upper molar postprotocrista and with a slight modification of the occlusal relationships of the upper and lower molars.

H. morinionensis also appears to differ from *H. quercyi* in having a buccally salient M^3 parastyle. The possibility cannot be excluded that this was broken in Teilhard's figured specimen. Two other characters, depth of M^2 ectoflexus and shape of the M_3 hypoconulid, may be intraspecifically variable. The first is supported by two M^2s of an undescribed species from Hordle Cliff, where the difference in depth is at least as great as between the Creechbarrow and Aubrelong 2 specimens. The second is supported by two specimens of *H. armatus* from Bouxwiller in the NMB (Bchs490 and Bchs306): the former is like the holotype (see Stehlin 1916: text-fig. 346b) where the hypoconulid is buccally situated and projecting and the lobe is short; the latter has a much longer median hypoconulid lobe.

Given the above conclusions, *H. morinionensis* is closely related to *H. quercyi* and is a good candidate both morphologically and stratigraphically to be its ancestor. *H. morinionensis* has no known specialized characters which would prevent such a possibility.

Heterohyus spp. indet.
(Text-fig. 40G–W)

MATERIAL. Six incisor fragments (M35699–700, M35708, M37116–8).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. These specimens show size differences, and some confusing morphological differences at least some of which are ontogenetic.

M35708 is much smaller than any of the others and almost certainly belongs to *H.* aff. *nanus* as represented by the M_2. It is rolled and the distal enamel band is little wider than the mesial one. The former was probably once wider, being worn away parallel to the buccal edge by post-mortem abrasion (Text-fig. 40U–W).

All the other incisor fragments are essentially the same size and presumably belong to the commoner *H. morinionensis* or to *H.* cf. *sudrei*, or both. The morphology of *Heterohyus* incisors has not been covered in much detail by authors and it is possible that they are not distinctive at species level. *H. sudrei* has no incisors attributed to it, whereas they are known for most of the other named species. The Creechbarrow incisors vary in width of the distal enamel band and cross-sectional shape.

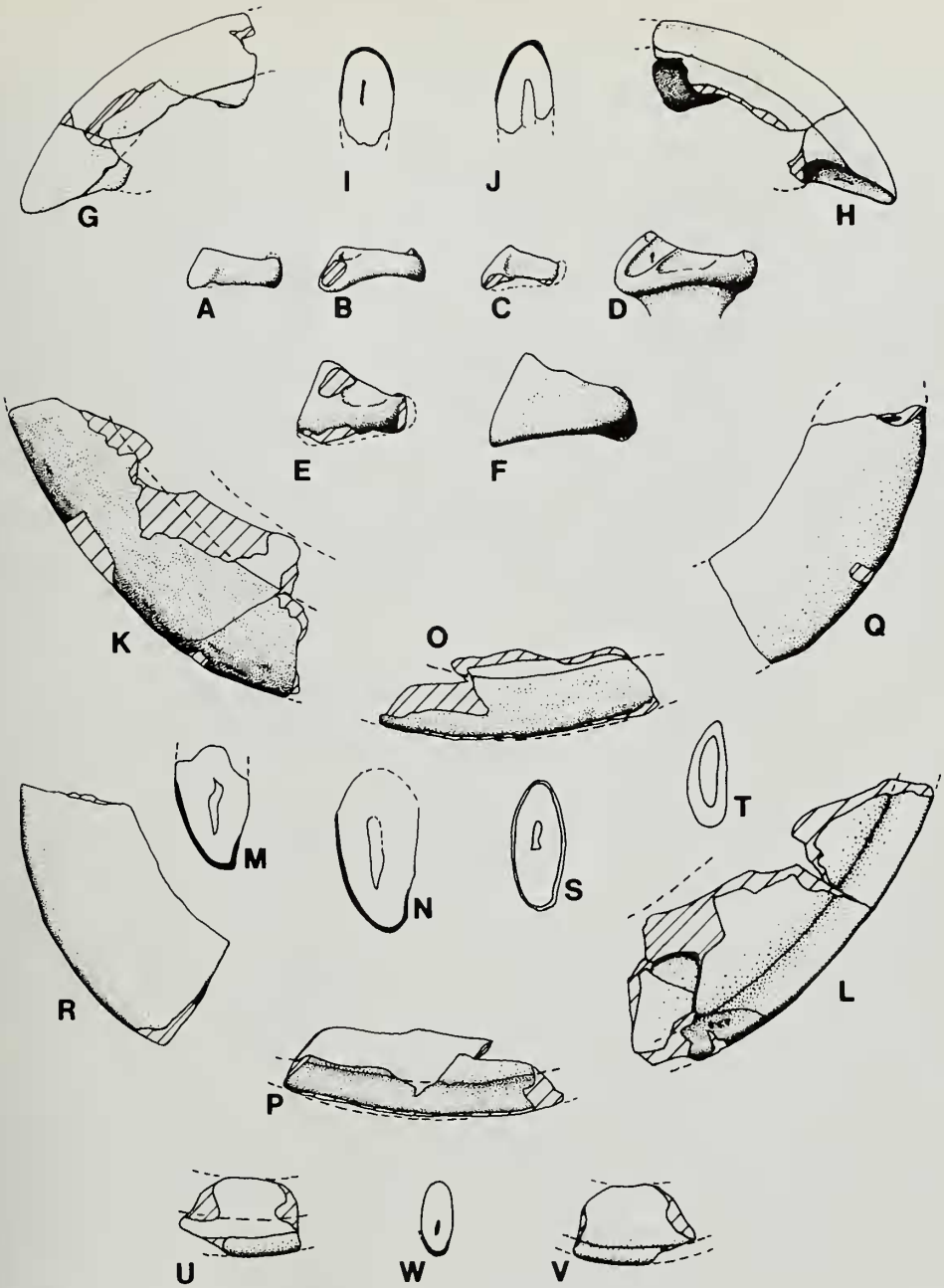
M35700 is the largest fragment. It is truncated at both ends but can be orientated by the apical narrowing of the pulp cavity. The enamel is slightly rugose, the distal enamel band is wide and the mesial enamel band concave. Apically there is a sharp mesiobuccal angle, but passing basally this angle becomes slightly rounded and begins to migrate lingually, thus making the buccal edge more evenly rounded and narrowing the mesial concavity. At this point, the mesial enamel has a noticeably pitted surface (Text-fig. 40K–N).

M35699 is a small fragment which appears to correspond in position to the apical end of M35700.

In M37117, the buccal edge, although rather eroded, appears to have been rounded without a sharp mesiobuccal edge; the mesial enamel band is flat; and the distal enamel band is about two-thirds the width of that of M35700. In incisors of *H. nanus* and *H. quercyi*, at least, the distal enamel band narrows in a basal direction. It thus seems reasonable to suggest that M37117 represents a more basal region than M35700 (Text-fig. 40O–P).

M37116 is rather eroded but has a complete layer of cement, is a thin oval in cross section and tapers basally. It is thus considered to be a root fragment. Basally the pulp cavity is open but is reduced apically to a small lumen and must thus represent an old individual (Text-fig. 40Q–T).

M37118 is a crown fragment which differs significantly from the others (Text-fig. 40G–J). It preserves the naturally worn tip and its mesial enamel band is convex, not concave, for most of



Text-figure 40 *Heterohyus* teeth. **A–F**, distal views of lower preultimate molars, ×8. A, right M_1 (reversed) (UM MPR4) of *H. nanus* Teilhard from Malpérié; B, right M_2 (reversed) (UM RBN6004) of *H. nanus* from Robiac; C, left M_2 (M35709) of *H.* aff. *nanus* from Creechbarrow; D, right M_2 (reversed) (M35705) of *H. morinionensis* sp. nov. from Creechbarrow (f = facet caused by M^2 metacone); E, left $M_{1/2}$ (M35707) of *H.* cf. *sudrei* from Creechbarrow; F, right M_2 (reversed) (P. Louis collection ROB330) of *H. sudrei* Sigé from Robiac. (A, B and F drawn from casts). **G–W**, incisors of *H.* spp. indet. from Creechbarrow, ×4. G–J, ?upper right incisor crown fragment (reversed) (M37118); K–N, adapical crown fragment of lower left incisor (M35700); O–P, adbasal crown fragment of lower incisor (M37117); Q–T, root fragment of right lower incisor (reversed) (M37116); U–W, crown fragment of lower incisor (M35708). G, K, O, Q and U are distal views; H, L, P, R and V are mesial views. I, J, M, N, S, T and W are transverse sections, shown as if of left teeth and viewed basally, so that distal is to the left and mesial to the right; I, M and S are from apical ends, J, N and T from basal ends; enamel is shown as solid black and cement is delimited by a double line.

its length. It could represent a different taxon. However, the occlusobuccal angle of the worn tip is much less acute than for lower incisors (see Teilhard 1922: text-figs 40b and 41; Stehlin 1916: text-figs 340, 349; Heller 1930: pl. 5, fig. 4a–c; and Sigé 1975: text-fig. 1b–c), as it is in rodents. Also the tooth is convex mesially as in the upper incisor ('I^1?') of *Apatemys* figured by Russell *et al.* (1979: pl. 1, fig. 10). These facts support it being an upper incisor (I^1), in contrast to all the other fragments which are lowers (I_1).

Upper incisors of only two specimens of *Heterohyus* have been described and figured. One is that of the lost skull of *H. quercyi*; the other is an isolated I^1 cusp tip fragment from Mutigny (Russell *et al.* 1979: 227; pl 3, fig. 8). The latter was provisionally attributed on the basis of differences from those belonging to *Apatemys* from the same locality. Whereas the Mutigny I^1? has a complete enamel crown and is bicuspid like *Apatemys*, that of *H. quercyi* is, according to Teilhard, 'sciuroïde, émaillée sur sa face externe'. Under these circumstances, it seems unlikely that the I^1 of *H. quercyi* was bicuspid at least during most of its life. M37118 at its basal end is beginning to develop a sharp mesiobuccal edge. Like the lower incisors the enamel is slightly rugose. The worn tip is obliquely bevelled, wear being more intense mesially than distally.

If the different types of lower incisor fragment indeed represent successive segments, the minimum length for this tooth measured along the curvature would be 30 mm. A more realistic estimate, based on more gradual narrowing of the distal enamel band, would be 40 mm. From the size of the pulp cavity in M35700 compared to M37116, it is likely that the root remained open until a fairly advanced wear stage.

Order **CARNIVORA** Bowdich 1821

Superfamily **MIACOIDEA** Cope 1880
(rank emend. Simpson 1931)

Family **MIACIDAE** Cope 1880

Subfamily **MIACINAE** Cope 1880
(rank emend. Trouessart 1885)

TYPE GENUS. *Miacis* Cope 1872.

INCLUDED GENERA. *Uintacyon* Leidy 1872; *Tapocyon* Stock 1934; *Vulpavus* Marsh 1871; *Vassacyon* Matthew 1909; *Oodectes* Wortman 1901; *Paroodectes* Springhorn 1980; *Palaearctonyx* Matthew 1909; *Pleurocyon* Peterson 1919.

RANGE. Eocene, North America and Europe; Upper Oligocene, Asia?

DIAGNOSIS. See Matthew (1909: 345).

COMMENT. Miacines are generally rare in European Eocene faunas. They have been described mainly by Filhol (1876*a*), Teilhard (1915), Guth (1964), Beaumont (1966), Quinet (1968), Rich (1971) and Springhorn (1980, 1982). Flynn & Galiano (1982) have shown the Miacoidea and Miacidae to be paraphyletic, but have not resolved the interrelationships of the now caniform 'Miacinae', although they have added other genera. The old classification is thus retained as a conservative measure.

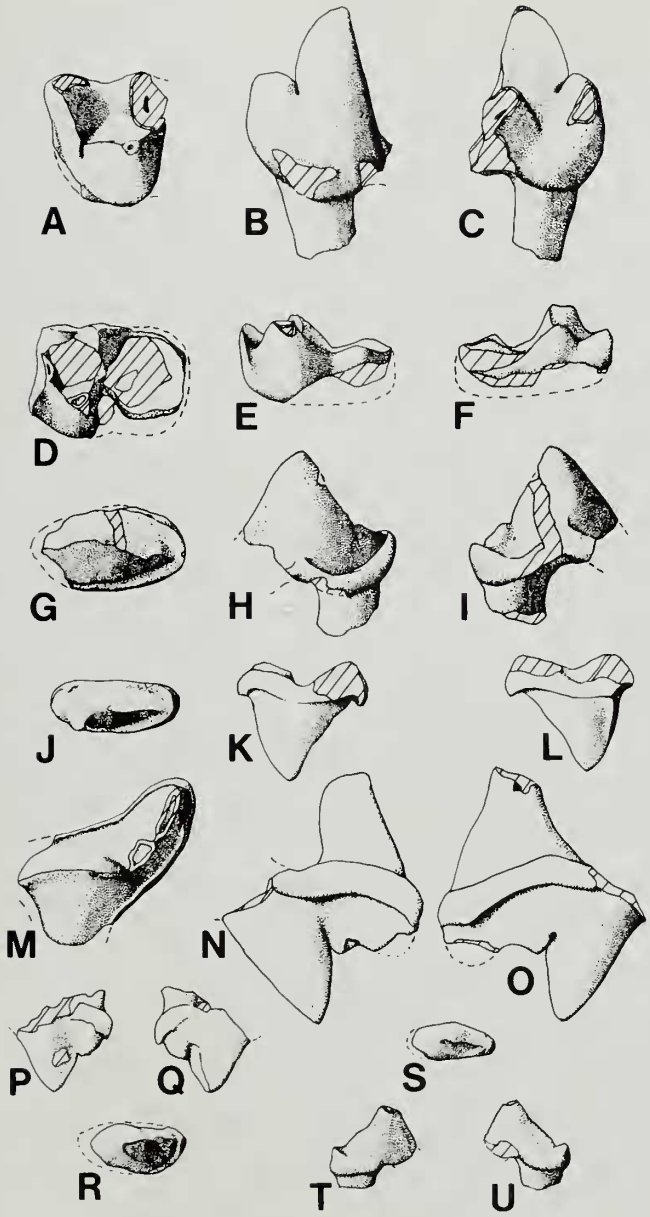
Genus ***MIACIS*** Cope 1873

?***Miacis*** sp. indet.
(Text-fig. 41A–O)

v. *1977b* Miacidae indet.; Hooker: 141.
vp. *1980* Miacidae indet.; Hooker & Insole: 41.

MATERIAL. Right P^2 (M36206); right and left P^4s broken mesially (M36207–8); right P_4 (M36202); three left M_1 trigonid fragments (M36210–1, M37568); right M_2 (M37569).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.



Text-figure 41 Miacinae teeth. A–O, ?*Miacis* sp. indet. A–C, left M_1 trigonid fragment (M37568); D–F, right M_2 (reversed) (M37569); G–I, right P_4 (reversed) (M36202); J–L, right P^2 (reversed) (M36206); M–O, right P^4 (reversed) (M36207). P–U, Miacinae indet. P–R, Left P^3? (M36204); S–U, right P_3? (reversed) (M36200). A, D, G, J, M, R and S are occlusal views. B, E, H, K, N, P and U are buccal views. C, F, I, L, O, Q and T are lingual views. All are from Creechbarrow; ×6·6.

DESCRIPTION. The association of these few broken isolated teeth is arbitrary. The size ratios of the different tooth types fit *Miacis*, but depend on this association. The form is very similar in size to *Miacis exilis* (Filhol 1876*b*) Teilhard 1915 from the Phosphorites du Quercy.

P^2: This tooth is 2·7 mm long and 1·2 mm wide. It fits Guth's (1964: 360) description of that of *M. exilis* in the complete cingulum and its development distally into a metastyle (Text-fig. 41J–L). The preparacrista curves lingually to join the lingual cingulum halfway between the paracone and the mesial tooth margin. A faint parastyle is represented by a slight cingular swelling.

P^4: M36208 only preserves the metastylar wing. M36207 only lacks the protocone and parastyle, if there was one (Text-fig. 41M–O). The cingulum is strong and continuous and the enamel has faint wrinkles which are orientated vertically. M36207 appears to have a longer metastylar wing than do the miacine P^4s from the Sparnacian of Dormaal figured by Quinet (1968: pl. 6, figs 5–9) and also *M. exilis* (Guth 1964: pl. 15, top left fig.). It is similar to a miacine P^4 from Mormont (LGM 40937) but here the buccal cingulum is interrupted at the paracone.

P_4: This tooth is 1·8 mm wide. It is broken in the parastylid region (Text-fig. 41G–I). The cingulum appears to have been complete buccally but incomplete lingually. The small hypoconid is low and distal on the distal protoconid crest and salient only lingually; it is, however, larger than on any of the *M. exilis* P_4s figured by Teilhard (1915: 112, text-fig. 2) or by Guth (1964: pl. 15, top right fig.).

M_1: Of the three trigonid fragments, two are too corroded or broken to be worthy of description. M37568, however, is better preserved but has the metaconid broken (Text-fig. 41A–C). It is 2·7 mm wide. The buccal cingulum extends for only a short distance between the paraconid and protoconid. The paraconid has a bluntly keeled mesial edge. The distal edge of the trigonid is nearly vertical and the metaconid was probably as high or higher than the paraconid. In occlusal view the mesiolingual corner is acute, resembling in this way Guth's (1964: pl. 16) top right rather than top central figure of *M. exilis*. This feature thus appears to be of only individual significance.

M_2: This tooth is broken and corroded basally, especially round the talonid and in the trigonid and talonid basins (Text-fig. 41D–F). It nevertheless shows much lower trigonid cusps than the M_1, the paraconid and metaconid being subequal. A prominent cingular spur occurs on the mesiobuccal corner. Of Guth's (1964: pl. 16) occlusal views of *M. exilis* lower molars, in cusp pattern M37569 most closely resembles the top left figure; the other two have a more oblique arrangement. It is estimated to have been 3·2 mm long and 2·4 mm wide.

DISCUSSION. Too little is known of this form to be more precise about its affinities, but it testifies to the presence of at least one stoat-sized carnivore in the Creechbarrow fauna.

?Miacinae, gen. et sp. indet.
(Text-fig. 41P–U)

MATERIAL. Left P^3? (M36204); right P_3? (M36200).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DISCUSSION. These rather undiagnostic teeth indicate the probable presence of a second miacine in the Creechbarrow fauna, a little more than half the size of ?*Miacis* sp. indet. The left P^3? is estimated at 1·1 mm wide. The right P_3? is 0·8 mm wide.

Order **CONDYLARTHRA** Cope 1881

Family **PAROXYCLAENIDAE** Weitzel 1933

TYPE GENUS. *Paroxyclaenus* Teilhard 1922.

INCLUDED GENERA. *Kopidodon* Weitzel 1933; *Vulpavoides* Matthes 1952 (including *Russellites* Van Valen 1965); *Pugiodens* Matthes 1952 (doubtfully distinct from *Vulpavoides*); *Spaniella* Crusafont-Pairo & Russell 1967; ?*Kochictis* Kretzoi 1943.

RANGE. Sparnacian to Bartonian, possibly to Ludian or even to Chattian (*Kochictis*), Europe. The Asian record based on *Dulcidon* Van Valen 1965 has been removed by Tobien (1969: 30–31).

DIAGNOSIS. See Van Valen (1965: 389).

DISCUSSION. This small, rare, endemic European family numbers less than twenty published specimens. Fortunately three of the genera are known from skulls with nearly complete dentitions and in addition there are several skeletons from Messel. The most recent detailed studies are by Tobien (1969), Rich (1971) and Koenigswald (1983). The small number of specimens means that the degree of intraspecific variation is virtually unknown in most cases, with consequent disagreement among authors on intrageneric variation also (see below).

Van Valen's (1965, 1967) rank of family is followed here. Tobien (1969) ranked it as a subfamily of the Arctocyonidae. Ordinal affinity follows Russell & McKenna (1962) and Tobien (1969), rather than Van Valen (1965) who placed them with a query in the Insectivora. Generic content essentially follows Tobien (1969) except that *Russellites* is synonymized with *Vulpavoides*.

Genus *VULPAVOIDES* Matthes 1952

[incl. *Russellites* Van Valen 1965, ? = *Pugiodens* Matthes 1952]

TYPE SPECIES. *V. germanica* Matthes 1952. Early Lutetian, Geiseltal, D.D.R. (? = *Pugiodens mirus* Matthes 1952; see Van Valen 1965, Tobien 1969).

INCLUDED SPECIES. *V. simplicidens* (Van Valen 1965) comb. nov.; *V. cooperi* sp. nov.

RANGE. Early Lutetian, D.D.R.; middle Lutetian, France; late Lutetian, Switzerland; and Marinesian, England.

EMENDED DIAGNOSIS (modified from Van Valen, 1965: 392). Upper molars relatively short (length from 58–75% of width) with: cusps moderately high (M^1 paracone height from crown base from *c.* 90–100% of tooth length); paracone and metacone relatively close together; postmetaconule crista weak to absent; paraconule weak to absent; metaconule weak; postprotocrista confluent with metaconule; strong centrocrista not strongly indented buccally or lingually; preparaconule crista absent; ectoflexus weak to moderate. P^{3-4} with: metacone present; and lingual half much shorter than buccal half. Note that the premolar characters are known only for the type species.

DISCUSSION. Van Valen (1965: 390) synonymized *Vulpavoides germanica* (based on a crushed cranium with upper dentition) with *Pugiodens mirus* (based on a mandibular ramus with lower dentition) on similarity of occlusal relationships. The choice of the latter as the senior synonym was probably to avoid the suggestion of unjustified miacid relationships implied by the alternative *Vulpavoides* (i.e. like *Vulpavus*). It was unfortunate, however, as the mandible was already lost (Van Valen 1965: 391) and could not be located when I visited Halle in 1979. Tobien (1969: 28, 35) gave reasons for a certain amount of doubt regarding the synonymy of the two genera and preferred to use *Vulpavoides* as the senior synonym. If the synonymy is accepted, then Van Valen should be followed as 'first reviser' according to the ICZN rules (1985: 53). *Vulpavoides* is used here because of doubt over synonymy and the present restriction of comparisons to the upper teeth.

Van Valen (1965: 392) considered his new genus *Russellites* to be the one most closely related to *Pugiodens* (his sense), yet distinct. He later (1967: 259) synonymized it without comment with *Pugiodens*. Tobien (1969: 29) considered it distinct and to share a number of characters with *Kopidodon* not shared with *Vulpavoides*: i.e. P^4 not transversely elongated; M^2 outline identical; M^2 distobuccal corner not rounded and mesiobuccal corner projecting; M^2 buccal edge perpendicular to transverse axis; and less reduction of M^3.

However, the P^4 character based on the roots does not necessarily indicate a similarity with the very characteristic massive crown without metacone in *Kopidodon*. Also, the orientation of the buccal edge to the transverse axis shows some individual variation. In the holotype M^1 of

V. germanica it is perpendicular. In the M^1 figured by Heller (1930: pl. 1, fig. 3a–b), it is oblique, the mesiobuccal angle being obtuse. In the holotype M^1 of '*R.*' *simplicidens*, the buccal edge is perpendicular, but in NMB Bchs656 (M^1) from Bouxwiller, it is oblique, the distobuccal angle being obtuse. Furthermore the M^2 outlines in *Kopidodon* and *Russellites* are not exactly identical. The remaining characters can be more than matched by the following which are shared between *Russellites* and *Vulpavoides* but not with *Kopidodon*: upper molars with postmetacrista low, outline short and broad with paracone and metacone consequently closer together, strong centrocrista not strongly indented buccally or lingually and preparaconule crista absent.

Vulpavoides cooperi sp. nov.
(Text-fig. 42A–D, I–K)

v. *1977b Russellites* sp.; Hooker: 141.
v. *1980 Pugiodens* sp.; Hooker & Insole: 42.

Name. After Mr J. Cooper, for help with field work.

Holotype. Right M^1, M37570. Text-fig. 42A–D.

Doubtfully referred specimen. Left DP^4? fragment (M35646).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Diagnosis. Small *Vulpavoides* (M^1 3·0 mm long × 5·2 mm wide); M^1 relatively short and broad (length 58% of width); with no paraconule; paracone and metacone close together; high preprotocrista joining paracone lingually; crestiform metaconule forming buccal end of postprotocrista; no postmetaconule crista; sloping height of slightly worn paracone equal to the tooth length. Ectocingulum and ectoflexus weak.

Differential diagnosis. *V. germanica* Matthes is larger with stronger upper molar ectocingulum and deeper ectoflexus. *V. germanica* and *V. simplicidens* (Van Valen) have relatively longer M^1 with lower, more widely spaced paracone and metacone, cuspate paraconule and metaconule present; postmetaconule crista low; and low preprotocrista reaching only to paraconule.

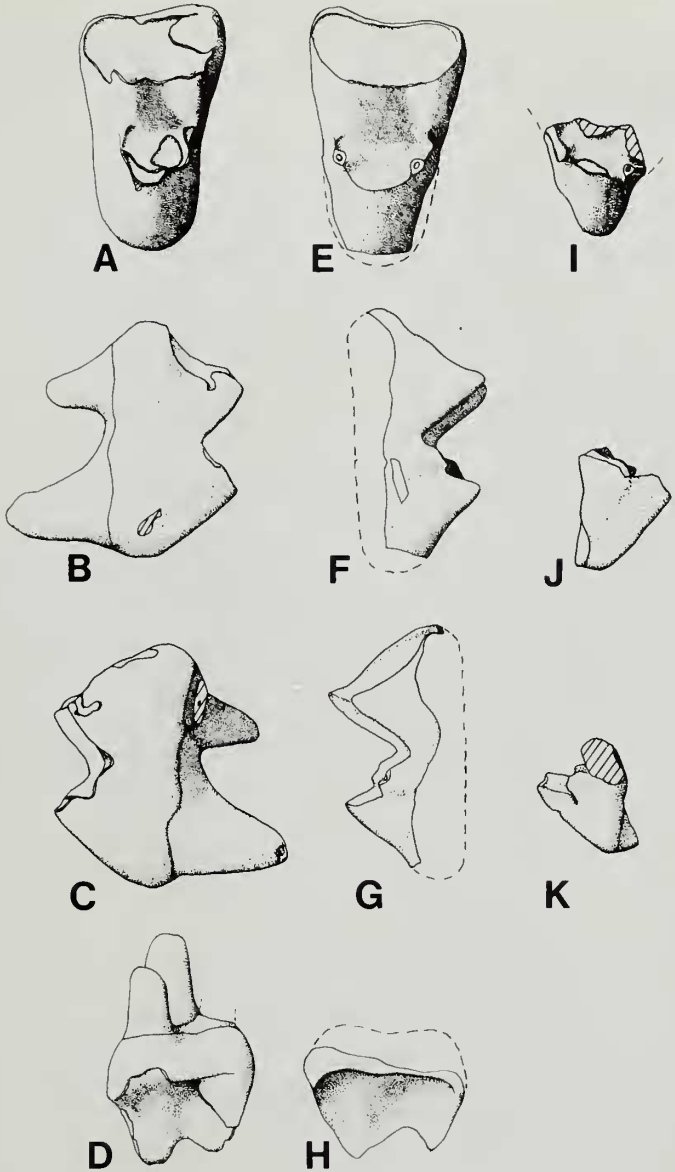
Description and discussion. M37570 is considered to be an M^1 as it has an oblique buccal edge with an obtuse mesiobuccal angle. M^2s and M^3s have acute mesiobuccal angles.

There are no sharply delimited wear facets but dentine is exposed on the protocone, metaconule, paracone and metacone and also in the trigon basin and extensively over the stylar shelf, the latter merging with that on the paracone and metacone. A buccal phase facet on the distal side of the metacone suggests an angle of shear with the M_2 trigonid of about 45°. Similar smooth enamel surfaces but with no definable edges occur on the mesial side of the metacone and on both sides of the paracone.

The holotype is compared in Text-fig. 42 with the referred M^1 of *V. simplicidens* from Bouxwiller. The weak ectocingulum is similar in both and contrasts with the stronger one in *V. germanica*. The obliquity of the protocone is also like *V. simplicidens*, but M^1 of *V. germanica* is too worn to compare for this character.

One of the most striking features of M^1 of *V. cooperi* is the partial zalambdodonty. This is not so much the result of independent drawing together of the paracone and metacone, as rather an accommodation response of these cusps to extreme differential shortening of the tooth as a whole. Nevertheless, the mesocylix (the occlusal cavity within an upper molariform tooth) is very shallow buccally and must have occluded with an M_1 with a very reduced talonid. In the Eutheria, partial to complete zalambdodonty is common in palaeoryctoids, creodonts, various lipotyphlan families (see Van Valen 1966, Butler 1972), anagalids and possibly dinocerates (Matthew 1928: 970). In the Condylarthra it appears otherwise to occur in the Mesonychidae.

No milk teeth have hitherto been recorded for paroxyclaenids, but M35646 may be a DP^4 as it has relatively thinner enamel than M37570 but a somewhat similar cusp pattern (Text-fig. 42I–K). Only the lingual half is preserved, but the protocone has the same oblique orientation



Text-figure 42 *Vulpavoides* teeth. A–D, **holotype** right M^1 (reversed) (M37570) of *V. cooperi* sp. nov. from Creechbarrow. E–H, left M^1 (NMB Bchs656) of *V. simplicidens* (Van Valen) from Bouxwiller, drawn from cast. I–K, left DP^4? fragment (M35646) of *V. cooperi*? from Creechbarrow. A, E and I are occlusal views. B, F and J are mesial views. C, G and K are distal views. D and H are buccal views. All × 6·6.

and long lingual slope. It differs in the more sharply acute lingual outline, and presence of a paraconule which is buccal to the metaconule, both being isolated by clefts from the protocone. There is the faintest suggestion of a postparaconule crista.

Although only the holotype is definitely referrable to this taxon, its distinctness and the rarity of all members of the family Paroxyclaenidae are considered sufficient justification for description of a new species on an isolated M^1.

Little can be said of the relationships to the other species of the genus, but *V. simplicidens* of middle to late Lutetian age is a potential ancestor for *V. cooperi*. The minimum changes required would be molar shortening, accompanied by conule reduction and paracone and metacone height increase. *V. simplicidens* has no known specialized characters which would prevent such a relationship.

Order **CETACEA** Brisson 1762

Suborder **ARCHAEOCETI** Flower 1883

Family **DORUDONTIDAE** Miller 1923

Genus ***ZYGORHIZA*** True 1908

Zygorhiza wanklyni (Seeley 1876) Kellogg 1936

* 1876 *Zeuglodon Wanklyni* Seeley: 428–432.
v. 1907 *Zeuglodon Wanklyni* Seeley; Andrews: 124–127, fig. 1.
? *1933 Zeuglodon wanklyni* Seeley; Burton: 161.
v. 1936 *Zygorhiza? wanklyni* (Seeley) ?Kellogg: 174–175.
v. 1972 *Zygorhiza wanklyni* (Seeley); Halstead & Middleton: 186–187, text-fig. 1.
v. *1980 Zygorhiza wanklyni* (Seeley); Hooker & Insole: 41.

The history of occurrence of this whale from the Barton Clay of Barton has been fully reviewed by Halstead & Middleton (1972). In summary, the holotype skull is lost and referred material is restricted to a few isolated vertebrae. It is worthy of note that a series of about two dozen associated vertebrae is in the collections of the Bournemouth Natural Science Society. They are currently being conserved by Paul Clasby of Lymington and will be the subject of a joint project when the conservation work is finished.

Detailed stratigraphical information is not recorded with any of these specimens, but the abundance of glauconite grains on all except M12346 (figured Halstead & Middleton, 1972: text-fig. 1) strongly suggests the range of beds B–D as the provenance. M12346 may be from beds E or F as its matrix consists of non-glauconitic clay.

Family **BASILOSAURIDAE** Cope 1867

Genus ***BASILOSAURUS*** Harlan 1834

Basilosaurus sp. indet.

v. 1972 *Basilosaurus* sp. indet.; Halstead & Middleton: 187–189, text-figs 2–3.
v. *1980 Basilosaurus* sp.; Hooker & Insole: 41.

No new specimens have come to light from the Barton Clay of Barton since Halstead & Middleton's (1972) record, but I call attention to a minor inaccuracy on p. 187 of their paper. Like most of the *Zygorhiza* specimens, the *Basilosaurus* vertebra, M26552, collected by Ken Hobby, has abundant adherent glauconite grains indicating a provenance from beds B–D, not bed E as stated. A personal communication from Mr Hobby shortly after he made the find in 1966 supports this provenance, although the specimen was not actually found *in situ* but on the slopes of Barton Cliff east of Chewton Bunny. The absence of glauconite grains from the other vertebra (M26553), collected by Paddy Blackwell, suggests a provenance of beds E–F (cf. D or E according to Halstead & Middleton, 1972: 189).

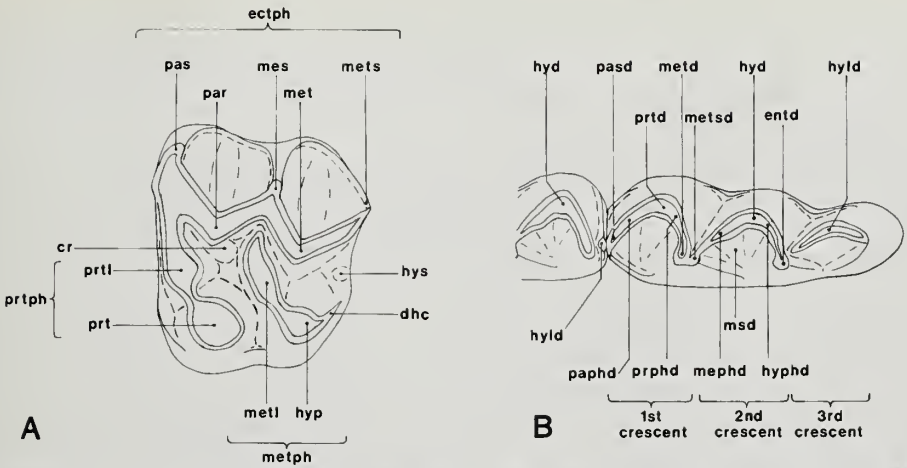
Order **PERISSODACTYLA** Owen 1848*b*

Superfamily **EQUOIDEA** Hay 1902

Family **PALAEOTHERIIDAE** Bonaparte 1850 (*sensu* Remy 1967)

TYPE GENUS. *Palaeotherium* Cuvier 1804.

INCLUDED GENERA. *Pachynolophus* Pomel 1847*a*, *Anchilophus* Gervais 1852, *Propachynolophus* Lemoine 1891, *Propalaeotherium* Gervais 1849, *Lophiotherium* Gervais 1859, *Paraplagiolophus*



Text-figure 43 Dental nomenclature of palaeotheriid cheek teeth. A, left upper molar. B, distal half of right M_2 and complete right M_3.

Abbreviations:

A. cr—rhinocerotoid crista
dhc—distal hypoconal crest
ectph—ectoloph
hyp—hypocone
hys—hypostyle
mes—mesostyle
met—metacone
metl—metaconule
metph—metaloph
mets—metastyle
par—paracone
pas—parastyle
prt—protocone
prtl—paraconule
prtph—protoloph

B. entd—entoconid
hyd—hypoconid
hyld—hypoconulid
hyphd—hypolophid
mephd—metalophid
metd—metaconid
metsd—metastylid
msd—mesoconid
paphd—paralophid
pasd—parastylid
prphd—protolophid
prtd—protoconid

Depéret 1917, *Plagiolophus* Pomel 1847*b*, *Leptolophus* Remy 1965 and *Pseudopalaeotherium* Franzen 1972.

Range. Late Ypresian to Stampian of Europe.

Genus ***PROPALAEOTHERIUM*** Gervais 1849

Type species. *Palaeotherium isselanum* Blainville 1864. Lutetian, Issel, Aude, France.

Included species. *P. helveticum* Savage, Russell & Louis 1965, *P. argentonicum* Gervais 1859, *P. rollinati* Stehlin 1905*a*, *P. hassiacum* Haupt 1925, *P. messelense* (Haupt 1925) Savage, Russell & Louis 1965, *P. parvulum* (Laurillard 1849) Depéret 1901, *P. sinense* Zdansky 1930 and ?*P. hengyangense* Young 1944.

Range. Early Lutetian–early Ludian?, Europe; late Eocene, China.

Diagnosis. See Savage *et al.* (1965: 57).

Propalaeotherium aff. ***parvulum*** (Laurillard 1849) Depéret 1901
(Pls 20–21; Text-fig. 44A; Table 25)

v. *1977b* *Propalaeotherium* cf. *parvulum* (Laurillard 1849); Hooker: 141.
v. *1979* *Propalaeotherium* cf. *parvulum* (Laurillard 1849); Kemp *et al.*: 102.
v. *1980* *Propalaeotherium* cf. *parvulum* (Laurillard 1849); Hooker & Insole: 42.

Holotype of *P. parvulum*. This is an M^3 from the Lutetian of Argenton, Creuse, France (Blainville 1839–64: genus *Lophiodon*, pl. 3), whose 'present location [is] unknown', according

to Savage *et al.* (1965: 66). Stehlin (1905*a*: 401) was also unable to locate this specimen but described and figured (1905*a*: text-fig. 25) three topotypes in Bordeaux Museum and the École des Mines, Paris (the latter now in the MNHN). Another topotype right M^3 similar to but more worn than the holotype (as figured by de Blainville) exists in the MNHN (unnumbered; cast in BM(NH) no. M42170).

Material. Right P^3 and left P^4, almost certainly associated (M36498), two P^3s (M37464, M37466), P^4 (M37465), $P^{3/4}$ (M37706), five M^3s (M35596–7, M37468–9, M37707), DP^4? in two non-fitting halves (M37467), P_2 (M37538), P_4 (M36176), five $M_{1/2}$s (M35598–9, M37470–2), M_3 (GM 978110–1; cast in BM(NH) no. M36493) and DP_2? (M37708).

Horizons and localities. The M_3 is from the Elmore Member, Barton Clay Formation, Elmore. The rest of the material is from the Creechbarrow Limestone Formation, Creechbarrow.

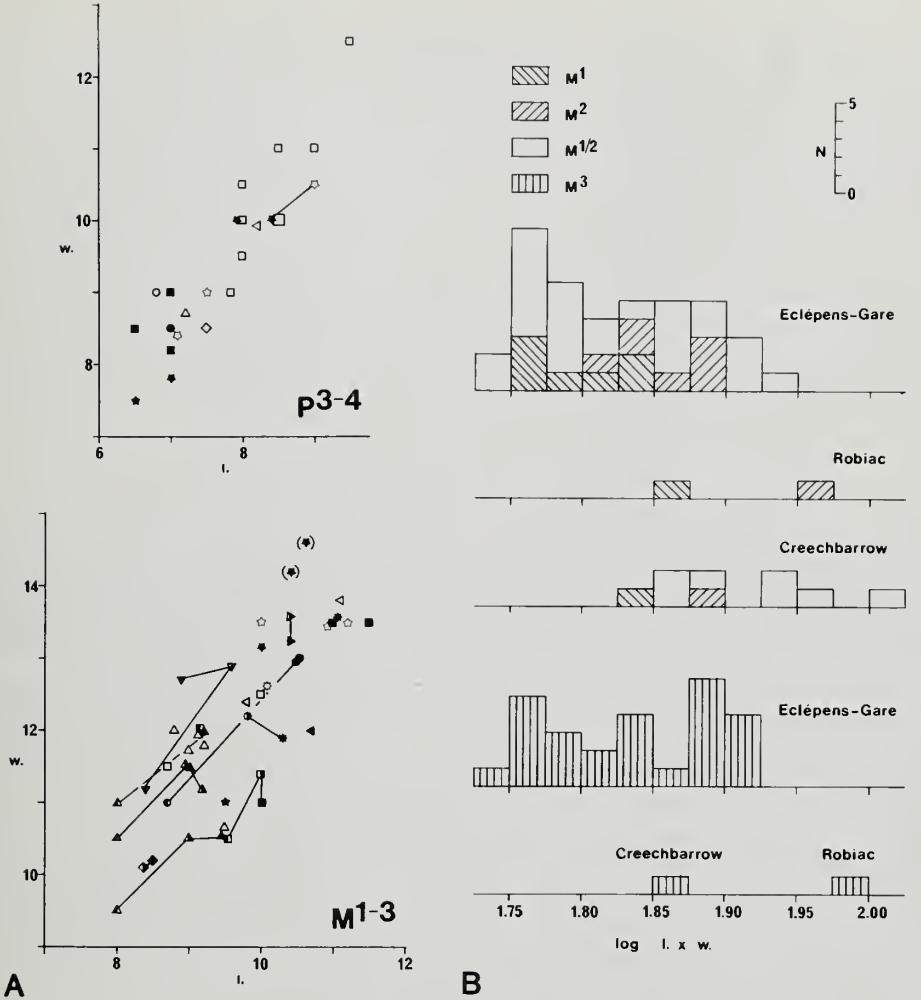
Diagnosis (quoted from Savage *et al.*, 1965: 66). 'Smaller animals referable to *Propalaeotherium*, comparable in size to very large individuals of *Hyracotherium* or of *Propachynolophus maldani* (estimated skull lengths: 140 to 160 mm). Upper molars with strong and somewhat bulbous mesostyles. Protoloph and metaloph with strong posterior flexure at labial extremity giving direct connection with paracone and metacone respectively. Upper premolars non-molariform, and with no mesostyles. P_4 may have incipient entoconid; otherwise lower premolars non-molariform'.

This appears to be the most recent diagnosis of the species. However, Stehlin's (1905*a*: pl. 9) figures show that the flexure of the protoloph and metaloph is by no means a constant feature, and that the upper distal premolars can show a moderate stage of molarization with small hypocones and mesostyles. In view of the uncertainties regarding the limits and definition of *P. parvulum*, no attempt will be made here to alter the diagnosis of Savage *et al.* (1965).

Authors' concept of the species. The name *P. parvulum* has tended to be used for all small Lutetian to Bartonian *Propalaeotherium*, not referable to *P. messelense*. Stehlin (1905*a*) frequently referred to the great variation in size and especially morphology in assemblages from Egerkingen, Chamblon and Mormont, some of which he referred to as varieties but without naming them. He (1905*a*: 430) was unable, however, to sort out these varieties into any groupings according to the different Egerkingen fissures or facies.

A study of Stehlin's (1905*a*: text-fig. 26; pl. 9) figures shows that there are quite striking differences in length/width proportions of the upper molars and distal premolars. There is also some tendency towards molarization in the case of the relatively longer P^4s (e.g. Stehlin, 1905*a*: pl. 9, figs 67, 70 in contrast with figs 1, 2, 45, 57). These differences become most marked when the material from Mormont and Creechbarrow is considered. Unfortunately these two localities have yielded few specimens.

The scatter diagrams in Text-fig. 44A are presented to show the extent of the differences in length/width proportions of P^3–M^3 from the different Egerkingen fissures and facies, and from Mormont (mainly from Stehlin's (1905*a*) measurements) and Creechbarrow (Table 25). Unfortunately there were very few measureable lower molars available to Stehlin and, whereas the majority of upper molars are from Egerkingen α, most upper premolars are from the aberrant facies. Nevertheless certain patterns seem to emerge. Upper molars of the Egerkingen γ fissure and grey marl and aberrant facies tend to be slightly larger than those from α and β fissures. Those from Mormont and Creechbarrow both plot bimodally for size and the larger specimens are relatively shorter and broader than the smaller specimens. Similarly, in the case of P^4, single specimens from α and β plot smaller than those from the grey marl and aberrant facies. The Mormont and Creechbarrow P^3s and P^4s are again bimodal but more on size and much less on proportions than are the upper molars; however, their total range is no greater than that of the aberrant facies P^4s. Two isolated $M_{1/2}$s from Creechbarrow are very similar in absolute size and proportions to those of Stehlin's (1905*b*: text-fig. 44) lower jaw (NMB Ec3), with P_{2-4}, M_{2-3}, referred to as 'Unbestimmbare Mandibularmaterialien kleiner Palaeohippiden von Egerkingen', but (1905*b*: 542) thought most likely to belong to 'einer der vielen Varietäten von



Text-figure 44 A, scatter diagrams of length (l) against width (w) of P^{3-4} and upper molars of *Propalaeotherium parvulum* (Laurillard) and *P.* aff. *parvulum* from various European localities. □ = Egerkingen grey marl facies; ○ = Egerkingen aberrant facies; ▽ = Egerkingen γ; △ = Egerkingen α; ◇ = Egerkingen β; ☆ = Eclépens-Gare; ☆ = Creechbarrow; ◁ = Lissieu; ✲ = Argenton; ▷ = Gentilly (Upper Calcaire Grossier). Of the upper premolars, solid symbols = P^3, outline symbols = P^4. Of the upper molars, symbols solid on left = M^1, on right = M^2 and completely solid = M^3; outline symbols = $M^{1/2}$. Measurements in millimetres. Lines join teeth of one individual. B, histograms of log. length × width of upper molars of *Lophiotherium siderolithicum* (Pictet) and the lectotype of *L. robiacense* Depéret, from Eclépens-Gare, Creechbarrow and Robiac. Original measurements in millimetres.

Propalaeotherium parvulum'. The lower molars of two other Egerkingen specimens (Stehlin 1905*a*: text-fig. 26; pl. 9, fig. 35) are relatively much narrower.

The greatest differences in size or length/width proportions of this material occur in the P^{3-4}s and M^3s, classically some of the intraspecifically most variable teeth (Gingerich 1974). Thus no convincing separation into two (or more) species can be made on the basis of these scatter diagrams. Until a more detailed synthesis is done of all the material (especially that from Egerkingen), it is best to accept only one species as occurring at any one time. Whether or not

Table 25 Length (l) and maximum width (w) measurements of *Propalaeotherium* aff. *parvulum* from Creechbarrow and Elmore. Measurements in millimetres.

No.	Tooth	l	w
M36498	P^3	8·4	10·0
M36498	P^4	9·0	10·5
M37464	P^3	7·9	10·0
M37466	P^3	7·0	7·8
M37465	P^4	7·1	8·4
M37707	M^3	10·0	13·2
M35596	M^3	10·6	(14·6)
M37468	M^3	10·4	(14·2)
M37538	P_2	7·2	4·3+
M36176	P_4	8·9	6·4
M35598	$M_{1/2}$	9·6	7·2
M37470	$M_{1/2}$	9·4	7·0
GM 978110–1	M_3	13·9	6·7
M37708	DP_2?	7·5	3·7

this should be considered conspecific with *P. parvulum*, based on material from the type locality, cannot be definitely decided here, hence the 'aff.' prefix to the English Bartonian specimens.

Description. Comparisons of the Creechbarrow material with the topotypes is restricted to upper molars. The Creechbarrow upper molars differ from the topotypes in having a deep fissure in the protoloph between the paraconule and protocone. This fissure is very shallow in the virtually unworn topotype $M^{1/2}$ figured by Stehlin (1905*a*: 401, text-fig. 25). It is evident from other upper molars from Argenton that the paraconule became fused to the protocone at an early wear stage. Upper molars from Eclépens-Gare (and Mormont undifferentiated, almost certainly also from Eclépens-Gare) are very similar to those from Creechbarrow in the depth of their protoloph fissure, as is the composite upper dentition from Lissieu figured by Depéret (1901: pl. 4, figs 2–3). Upper molars from Egerkingen are in general intermediate in the depth of this fissure but vary somewhat between the two extremes. Those from the younger fissures α and β appear similar in this feature to those from the older ones.

All the Creechbarrow M^3s are large and relatively short and broad, unlike the small and relatively more elongated M^3 from Mormont (Stehlin 1905*a*: pl. 9, fig. 68). Their mesostyles are also very strong.

The P^3s and P^4s can be divided into two morphological types:

	Type A	*Type B*
Outline:	Triangular	Subquadrate
Width/length ratio:	High	Low
Hypocone:	Absent	Present

In addition, type B teeth are smaller than type A teeth but not enough are available to test usefully the coefficient of variation. M37465 is fairly worn, closely resembles LM 46 from Mormont (Stehlin 1905*a*: pl. 9, fig. 67) but the hypocone appears larger; the wear makes judgement of cusp size difficult, but the remains of the lingual valley between the protocone and hypocone is nearly central on the lingual margin. M37466 is less worn, narrower lingually and with closer protocone and hypocone than M37465; unlike the latter there is also a metostyle which is distal to the midpoint of the ectoloph. Both M37465 and M37466 are type B teeth (Pl. 20, figs 1–2); the rest are type A (e.g. Pl. 20, figs 3–4).

The P_2 has no paraconid (Pl. 21, fig. 2). The metaconid is represented only by a slight lingual swelling halfway along the postprotocristid. There is a small hypoconid.

The P_4 is of roughly rectangular outline with protoconid and hypoconid in line mesiodistally (Pl. 21, fig. 3). The paralophid is weak, directed mesiolingually and dies out well buccal of the lingual margin. The entoconid is absent. In these features it is like NMB Ec3 from the Eggerkingen grey marl or aberrant facies (Stehlin 1905*b*: 541, text-fig. 44). NMB Ec1 from Eggerkingen α (Stehlin 1905*a*: 424, text-fig. 26) has semimolariform P_4, with a fairly large entoconid; strong convex paralophid continuous to the lingual margin; and talonid broader than trigonid.

The $M_{1/2}$s are also more like those of Ec3 than Ec1 in being relatively short and broad and in having the buccal crescents of trigonid and talonid more acute and the paralophid weaker (Pl. 21, fig. 4).

The M_3 is heavily worn. Its length/ width proportions are intermediate between those of Ec1 and Ec3. It also has an expanded hypoconulid lobe like Ec1.

The DP_2? is similar in general cusp arrangement to the non-molariform DP_2 (M35585) of *Lophiotherium siderolithicum* (see p. 352), but is longer and narrower; the talonid is lower, the entoconid being entirely missing; and the mesial slope of the metaconid is shallower, the base meeting the mesial end of the straight paralophid (Pl. 21, fig. 1).

Genus *LOPHIOTHERIUM* Gervais 1859

TYPE SPECIES. *Lophiotherium cervulum* Gervais 1859. Ludian, Euzet, Gard, France.

INCLUDED SPECIES. *L. pygmaeum* (Depéret 1901) Stehlin 1905*b* and *L. siderolithicum* (Pictet 1857) Depéret 1901 (?syn. *L. robiacense* Depéret 1917). Note that *L. magnum* Matthes 1977, *L. geiseltalensis* Matthes 1977 and *L. voigti* Matthes 1977 all appear to be synonymous with existing species of *Propalaeotherium*, but represent milk dentitions (see also Franzen 1980*b*: 91).

RANGE. Late Lutetian to Marinesian, Switzerland; Marinesian, England; Marinesian to Ludian, France; Ludian, Spain, Majorca.

DIAGNOSIS. See Savage *et al.* (1965: 72).

Lophiotherium siderolithicum (Pictet 1857) Depéret 1901
(Pl. 19, figs 8–9; Pls 22–23; Text-fig. 44B; Tables 26–27)

v. *1912* *Dictulumus leporinus* (Owen) (*sic*); Keeping: 130 (error for *Dichobunus leporinus*; in reality *Dichobune leporina* Cuvier).
v. *1977b* *Lophiotherium robiacense* Depéret; Hooker: 141.
v. *1980* *Lophiotherium robiacense* Depéret; Hooker & Insole: 42.

TYPES AND HISTORICAL BACKGROUND. Pictet (1857: 53–57; pl. 4, figs 1–3) described and figured a right maxilla with P^3–M^3 (the last tooth broken lingually) and figured (1857: pl. 4, fig. 4) an isolated worn upper right molar as representing his then new species *Hyracotherium siderolithicum*; he designated no types, so his two specimens were syntypes. Stehlin (1905*b*: 456) recognized the maxilla as the type and noted that it was lost; he did not mention the isolated molar. Following Stehlin's decision, therefore, the maxilla is recognized here as lectotype. Because it is such an advanced individual and virtually inseparable from typical maxillae in the type assemblage of *L. cervulum* from Euzet, Stehlin (1905*b*) referred it to this species. He also recognized, however, that the assemblage from Eclépens-Gare as a whole, although variable, was more primitive than typical *L. cervulum* yet more advanced than Lutetian *L. pygmaeum*. He therefore designated three phylogenetic stages A, C and E for *L. pygmaeum*, *L.* '*cervulum*' from Mormont (Eclépens-Gare) and *L. cervulum* from Euzet respectively. He thought that the mixing of the Mormont faunas (see Stehlin, 1903: 10–13) was the cause of such high morphological variation in the premolars, the type of *L. siderolithicum* thus being from a younger fauna and synonymous with *L. cervulum*. Depéret (1917) named the varieties *atavum*, *transiens* and *progressum* for individuals in the Euzet *L. cervulum* assemblage which resembled respectively Stehlin's stages A, C and E. He then gave the name *L. robiacense* to two specimens from Robiac, which he considered to represent the constant state of stage C.

Within Le Mormont, apart from a few teeth from St Loup, *L. siderolithicum* in fact is known

Plate 20 Light macrographs of upper cheek teeth of *Propalaeotherium* aff. *parvulum* (Laurillard) from Creechbarrow, × 4. a, buccal and b, occlusal views. Fig. 1a, b, left P^3 (M37466). Fig. 2a, b, left P^4 (M37465). Fig. 3a, b, right P^3 (reversed) (M36498). Fig. 4a, b, left P^4 (M36498, almost certainly same individual as Fig. 3). Fig. 5a, b, right M^3 (reversed) (M37707). See p. 343.

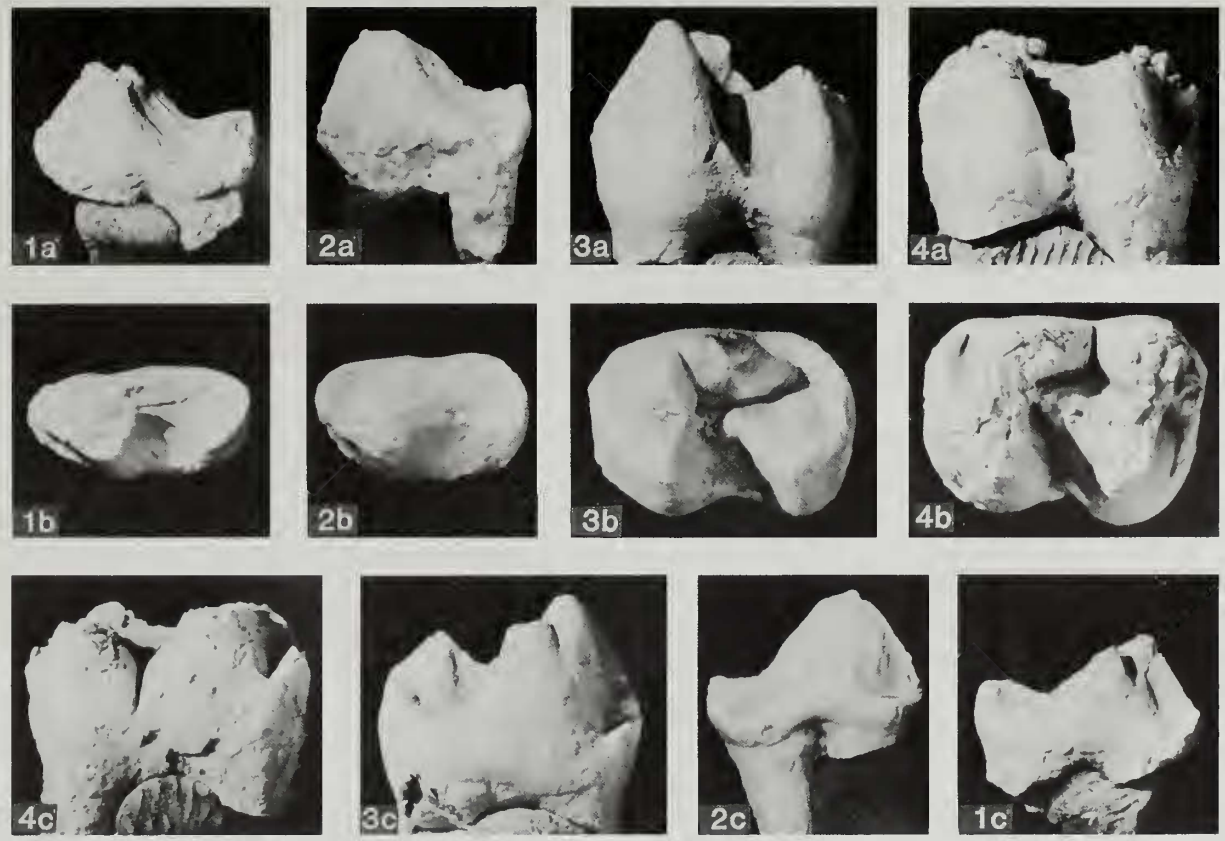


Plate 21 Light macrographs of lower cheek teeth of *Propalaeotherium* aff. *parvulum* (Laurillard) from Creechbarrow, ×4. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, left DP_2? (M37708). Fig. 2a–c, right P_2 (reversed) (M37538). Fig. 3a–c, left P_4 (M36176). Fig. 4a–c, left $M_{1/2}$ (M35598). See p. 343.

only from Eclépens, associated with an almost exclusively Marinesian mammal fauna (see Hartenberger, 1973: 68, for list), and de la Harpe (1869: 459) noted that out of five or six fissures in the quarry at Gare d'Eclépens, almost all of the animal fossils came from a single fissure. The degree of size variation is low (see Text-fig. 44B), supporting the idea that the old collections of Eclépens *L. siderolithicum* constitute essentially a single assemblage. Thus the high morphological variation recorded by Stehlin for the premolars of *L. siderolithicum* is considered to be an accurate representation of the species. The position is, however, unfortunately complicated in that other fissures were exploited after the time of de la Harpe and the specimens were not differentiated in the LGM collections (M. Weidmann, personal communication 1983).

The species name does not appear to have been used in major zoological literature since Depéret (1917). Savage *et al.* (1965) did not even include it in a synonymy list, considering that the Mormont material probably belonged to *L. robiacense*. They nevertheless doubted the constancy of the premolars of *L. robiacense*, the species being represented at most by two specimens. Sudre (1969*a*: 103–105, 118) pointed out that both specimens came from a very high level in the Robiac section which Roman (1904) considered to be lowest Ludian. As such, they are likely to be little older than the specimen from Fons 1 figured by Remy (1967) as *L.* aff. *cervulum*.

Remy (1967: 29–30) decided that species of *Lophiotherium* could only be determined on tooth morphology by statistical procedures, individual specimens being useless. He then showed that *L. pygmaeum*, *L. robiacense* and *L. cervulum* could be distinguished by P^{1-4}/M^{1-3} length ratio with no overlap. However, he was only able to measure one specimen of each of *L. pygmaeum* and *L. robiacense*; and the former is composite (Stehlin 1905*b*: 452, text-fig. 31).

It is considered here that the best procedure is to recognize *L. siderolithicum* as a statistically well-represented species, the type assemblage being essentially homogeneous, and a senior synonym of *L. robiacense* (if the two are identical).

Material. (54): Associated left P^4–M^2 (M36177); two P^1s (M37410–1); P^2 (M36497); two P^3s (M37412, M37703); two P^4s (M37413–4); twelve $M^{1/2}$s (SMC 9969, M35584, M36499,

Table 26 Length (l) and maximum width (w) measurements of *Lophiotherium siderolithicum* from Creechbarrow. Measurements in millimetres.

No.	Tooth	l	w	No.	Tooth	l	w
M37410	P^1	5·4	4·4	M37430	P_4	7·7	5·7
M36497	P^2	4·1	–	M37705	P_4	7·3	5·9
M37703	P^3	–	8·0	M37705	M_2	7·8	6·2
M37413	P^4	7·5	9·7	M37431	$M_{1/2}$	–	5·5
M36177	P^4	7·0	9·7	M37432	$M_{1/2}$	7·8	5·9
M36177	M^1	7·1	9·9	M37433	$M_{1/2}$	8·2	5·5
M36177	M^2	7·2	10·7	M37434	$M_{1/2}$	7·6	6·1
M35584	$M^{1/2}$	7·5	–	M37436	$M_{1/2}$	8·0	5·4
M37415	$M^{1/2}$	7·4	9·8	M35587	$M_{1/2}$	(7·3)	5·5
M37416	$M^{1/2}$	8·1	10·6	M37705	M_3	11·0	6·3
M37417	$M^{1/2}$	7·8	10·9	M37438	M_3	10·5	5·6
M37418	$M^{1/2}$	7·6	9·7	M37440	M_3	–	6·1
M37419	$M^{1/2}$	8·7	11·9	M37441	M_3	(11·0)	5·7
M37421	$M^{1/2}$	8·5	10·8	M37442	M_3	(11·0)	5·8
C9969	$M^{1/2}$	7·6	10·3	M36180	M_3	10·5	5·5
M36178	M^3	7·0	10·3	M35585	DP_2	6·6	4·1
M37424	M^3	–	10·6+	M35590	DP_3	–	4·5
M37426	DP^3	7·4	7·2	M37447	DP_3	7·4	5·0
M37427	DP^4	7·6	9·1	M37449	DP_3	–	5·6
M37428	DP^4	6·5	7·6	M35586	DP_3	7·6	5·0
M35588	P_4	7·0	5·3	M37451	DP_4	6·9	5·3
M37429	P_4	7·1	5·1	M37452	DP_4	7·7	5·3

M37415–23); three M^3s (M36178, M37424–5); upper molar fragment (M36179); DP^3 (M37426); three DP^4s (M37427–8, M37704); associated left P_4, M_{2-3} (M37705); five P_4s (M35588, M35594, M37429–31); eight $M_{1/2}$s (M35587, M35589, M37432–7); eight M_3s (M36180, M37438–44); two lower molar fragments (M35591, M37445); two DP_2s (M35585, M37446); six DP_3s (M35586, M35590, M37447–50); four DP_4s (M35592–3, M37451–2); lower canine (M36828).

Doubtfully referred material. (23): Two upper canines (M37453–4); twenty one incisors (M35595, M36228–35, M36237–8, M36792, M37455–63).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Emended diagnosis (modified from Savage *et al.* (1965: 79–80) for *L. robiacense*). Molariform upper teeth with very strong and discrete paraconules, weak to strong, indistinct to discrete metaconules; P^4 hypocone missing to as developed as protocone, usually moderately to well developed; P^3 hypocone missing or of height equal to protocone, poorly to well separated from it, usually moderately separated; P^2 hypocone missing or of height equal to protocone, poorly to moderately separated from it. P_4 entoconid moderately to strongly developed; P_3 entoconid weak to moderate; P_2 metaconid weak to strong.

Description. In tooth size the Creechbarrow assemblage is slightly larger than the Eclépens-Gare assemblage (see Text-fig. 44B) but there is much overlap. In morphology the two are very similar (Table 27), the latter having been described in detail by Stehlin (1905*b*).

In response to Remy's (1967) comments (see p. 350) I have attempted to divide into categories the grades of molariformity of the upper (those with the greatest number of easily recognizeable character states) premolars and score numbers of individual teeth for both assemblages. The different premolars are mainly isolated and often difficult to distinguish from one another. It seems possible to distinguish P^4s from P^3s because the latter have smaller, more mesial metaconules and are smaller overall. Moreover, they molarize differently: in P^4 the hypocone 'grows' gradually on the postprotocingulum, some distance behind the protocone, moving further distally in advanced stages; in P^3 the hypocone, from its moment of appearance, is the same height as the protocone and progressively buds off distally from it. P^2s molarize like P^3s and are difficult to separate except on smaller size and narrower proportions. P^1 is a small narrow wedge-shaped tooth with poorly differentiated protocone and hypocone. In Table 27, the number of specimens from both Eclépens-Gare and Creechbarrow and the lectotype of *L. robiacense* from Robiac are shown for each category of the four upper premolars. Although the peaks of the Creechbarrow character state distributions do not always correspond to those of Eclépens-Gare, they are not so skewed to one or other end of the scale as they are in *L. cervulum* or *L. pygmaeum*.

The isolated upper deciduous premolars (Pl. 22, figs 5–6) are identified as DP^3 and DP^4 and resemble those figured by Stehlin (1905*b*: 459, text-fig. 36) from Eclépens-Gare.

The lower cheek teeth from Creechbarrow also closely resemble those of the Eclépens-Gare assemblage, being only slightly larger (see Table 26 for measurements). Recognizing the different isolated lower premolars is difficult. Moreover, the fully molariform P_4s are very like M_1s or M_2s. Three molariform teeth from the left side of the jaw, from Hole 6 at Creechbarrow (Text-fig. 4, p. 209), have identical preservation and very similar wear states (Pl. 19, fig. 8). One is M_3; an M_2 can be associated with it by matching up interstitial facets; the third does not fit against the M_2 but is almost certainly from the same individual. Its hypolophid is weaker than that of M_2 and its entoconid, although well developed, is slightly lower than the metaconid. It is thus identified as P_4 and is as fully molariform as that of *L. cervulum* figured by Savage *et al.* (1965: 74, text-fig. 35c–d). Of three isolated teeth, identified as P_4, one is fully molariform like the Hole 6 one; another is worn but would have had the entoconid little more than half the height of the metaconid (Pl. 23, fig. 4); and a third is intermediate between the two.

Lower deciduous premolars are also difficult to separate from one another when isolated. Those here identified as DP_3 and DP_4 (e.g. Pl. 23, figs 2–3) are very similar to those figured by Stehlin (1905*b*: 469, text-fig. 39). An unworn non-molariform tooth with thin enamel and a

Table 27 Numbers of specimens in each character state of the four upper premolars, for assemblages of *Lophiotherium* at Eclépens-Gare and Creechbarrow. At right, condition in the lectotype of *L. robiacense* from Robiac.

Tooth	Category	Eclépens-Gare	Creech-barrow	Robiac
P^4	1. Hypocone undifferentiated on postprotocingulum	3	0	
	2. Hypocone very small on postprotocingulum	3	0	
	3. Hypocone smaller than protocone, postprotocingulum broken	8	0	1
	4. Hypocone = protocone, closer than paraconule to metaconule	3	2	
	5. Hypocone = protocone, same distance apart as paraconule and metaconule	6	1	
P^3	1. Hypocone undifferentiated on postprotocingulum	3	0	1
	2. Hypocone very close to protocone	7	1	
	3. Hypocone closer to protocone than paraconule to metaconule	9	1	
	4. Hypocone–protocone distance = paraconule-metaconule distance	4	0	
P^2	1.)	5	0	1
	2.} Same numbered categories as for P^3	4	1	
	3.)	5	0	
P^1	1. Metacone absent	2	0	
	2. Metacone small	4	0	
	3. Metacone subequal with paracone	0	1	1

papillate buccal cingulum between protoconid and hypoconid (M35585) is tentatively identified as DP_2. Its metaconid and metastylid are scarcely separated even at the tip, the entoconid is very small and mesial and distal parts are of approximately equal width (Pl. 23, fig. 1). As DP_2 it thus resembles *L. pygmaeum* more than it does *L. siderolithicum* as figured by Stehlin (1905*b*: 469, text-figs 38–39), and contrasts strongly with a more typical Creechbarrow DP_2 (M37446).

A palaeotherioid curved lower canine with a distal facet (M36828) (Pl. 19, fig. 9) resembles those of *L. cervulum* figured by Depéret (1917: pl. 15). It is of appropriate size to belong to *L. siderolithicum*. While attempting to identify miscellaneous canines from Creechbarrow, I noticed a strong resemblance between M36828 and the isolated canines described from Egerkingen and Mormont as *Choeromorus jurensis* Stehlin 1908 and *C. helveticus* Pictet & Humbert 1869 (particularly Pictet & Humbert 1869: pl. 25, fig. 11a). Because of their resemblance to miniature pig canines, these authors assumed that they were congeneric with the contemporary genus *Cebochoerus*, which was based on cheek teeth, and at that time placed in the family Suidae (now Cebochoeridae, p. 389). An anomaly was caused by the knowledge of certain tooth rows with typical *Cebochoerus* cheek teeth associated with non-*Choeromorus*-like canines. Stehlin 'resolved' the problem by assuming that the genera *Cebochoerus* and *Choeromorus* could only be distinguished on the canines as they had identical cheek teeth. Sudre (1978*b*: 52–54) discussed the problem in more detail and considered two other possible solutions: either that the canines of *Cebochoerus* were sexually dimorphic or that the canines attributed to *Choeromorus* belonged to another kind of animal. They have never been found *in situ* in a jaw with a *Cebochoerus* cheek dentition, so Sudre's second solution seems the more likely. In fact a close resemblance exists between Stehlin's (1908: 708, text-figs 101–102) two crucial specimens and the lower canines of *Anchilophus* cf. *dumasii* figured by Remy (1967: 23, text-fig. 13; pl. 5, fig. 1). *Anchilophus* occurs in both the Egerkingen and Mormont faunas identified on cheek

teeth and generic identity of the canines with these seems very likely. The strong pig-like curvature to these teeth was evidently to overcome accommodation problems in the long, shallow mandibular symphyses of both *Lophiotherium* and *Anchilophus*.

Two upper palaeotherioid canines of appropriate size and proportions are tentatively attributed to *L. siderolithicum*, as are various incisors which resemble those in Depéret's figures of *L. cervulum* (1917: pl. 15, fig. 9).

Conclusions. The presence of *L. siderolithicum* at Creechbarrow is good evidence of later Bartonian age. Its slightly larger size compared to the type assemblage might indicate either geographical differences or a temporal trend towards the even larger specimens from Robiac. There is no independent evidence either way, but the *Lophiotherium* lineage appears to have undergone no significant or directional change in size throughout its known stratigraphical range.

Genus ***PLAGIOLOPHUS*** Pomel 1847*b*

[= *Paloplotherium* Owen 1848*a*]

Type species. *Palaeotherium minus* Cuvier 1804. Première Masse du Gypse, Montmartre, Paris, France.

Included species. *P. cartieri* Stehlin 1904*b*, *P. lugdunensis* (Depéret & Carrière 1901), *P. cartailhaci* Stehlin 1904*a*, *P. annectens* (Owen 1848*a*), *P. fraasi* Meyer 1852, *P. javalii* (Filhol 1877*b*) (doubtfully distinct from *P. fraasi*) and *P. curtisi* sp. nov.

Range. Late Lutetian–Stampian, Europe.

Emended diagnosis (modified from Viret (1958: 359) and largely complementing Franzen's (1968: 16) diagnosis of *Palaeotherium*). Medium–small to medium–large Palaeotheriidae, cranium length 150–300 mm. DP^1 replaced by P^1 or both absent. Cheek teeth with or without cement; with high percentage of pericanalicular dentine (Remy 1976); and semihypsodont. Upper molars with buccal cusp height from 70–100% of tooth width and from 1·3–1·6 times the lingual cusp height. Upper molariform cheek teeth with prominent paraconules and high oblique metalophs. P^3 with or without metacone and without hypocone; P^4 with or without elongate metaloph and without hypocone; P_3 with or without hypoconid and without entoconid; P_4 with or without small entoconid and with high hypoconid. Successive molars increase in size distally. Lower cheek teeth with weak interrupted buccal cingulum; and lingual valley of first crescent deep. M_{1-2} with hypoconulid. Twinned metaconid/metastylid on molariform lower cheek teeth. Postcanine diastema medium short to medium long (lowers from 29–36% of cheek tooth row; uppers from 15–26% of cheek tooth row). Narial incision varying in depth from P^1 to M^1, the lower border consisting of premaxillae plus maxillae. Astragalus trochlear ridges at angle of 75° to navicular facet.

Plagiolophus curtisi sp. nov.

For type material, see under nominate subspecies. For synonymy, see under each subspecies.

Diagnosis. 1, small to medium-sized *Plagiolophus* (M^2 length 13·0–16·5 mm); 2, tooth cement absent; 3, P^1 present; 4, P^3 metacone present; 5, P^4 metaloph short, not reaching distal cingulum; 6, P^{3-4} metaloph nearly longitudinally orientated; 7, M^{1-2} distal hypoconal crest strong and longitudinally orientated; 8, upper cheek teeth with high distal cingulum; 9, upper molar paracone and metacone buccally salient; 10, upper molar metaloph obliquity medium; 11, molar crown height medium (height of buccal cusps ≃ maximum width of tooth); 12, upper molar buccal/lingual height ratio low; 13, upper molar protoloph fissure between paraconule and protocone moderately deep; 14, upper molar 'rhinocerotoid' crista present; 15, M^3_3 moderately distally expanded; 16, canines large and parallel orientated; 17, P_3 hypoconid present; 18, P_4 entoconid absent; 19, lower molar buccal/lingual height ratio 1 : 1; 20, molar enlargement gradient low. Muzzle broad anteriorly and mandibular symphysis narrow; palatal concavity

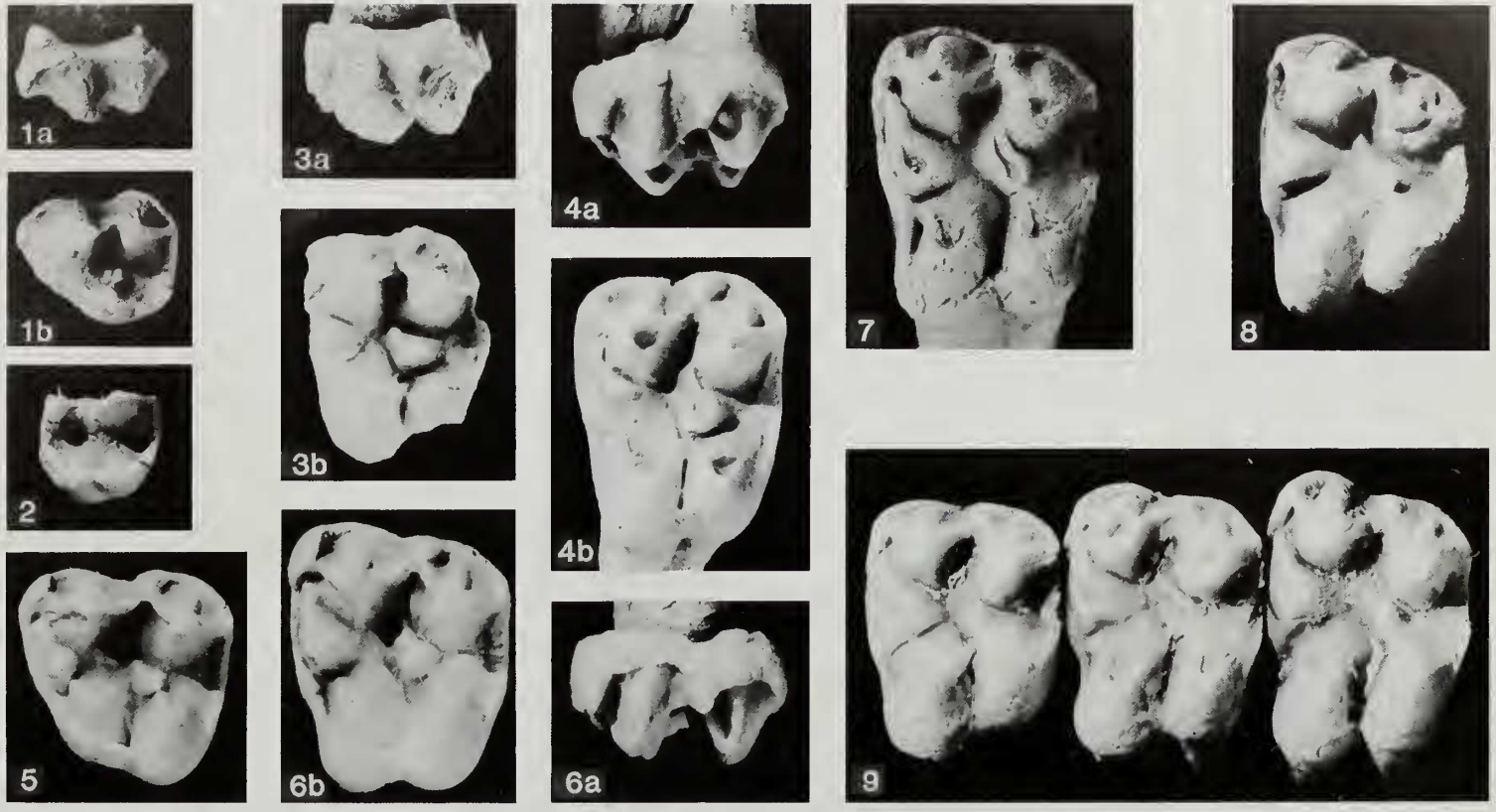


Plate 22 Light macrographs of upper cheek teeth of *Lophiotherium siderolithicum* (Pictet) from Creechbarrow, ×4. Views are buccal (a) and occlusal (b and unsuffixed). Fig. 1a, b, right P^1 (reversed) (M37410). Fig. 2, left P^2 (M36497). Fig. 3a, b, right P^3 (reversed) (M37703). Fig. 4a, b, left P^4 (M37413). Fig. 5, left DP^3 (M37426). Fig. 6a, b, left DP^4 (M37427). Fig. 7, left $M^{1/2}$ (SMC 9969). Fig. 8, right M^3 (reversed) (M36178). Fig. 9, left P^4–M^2 (M36177). See p. 347.

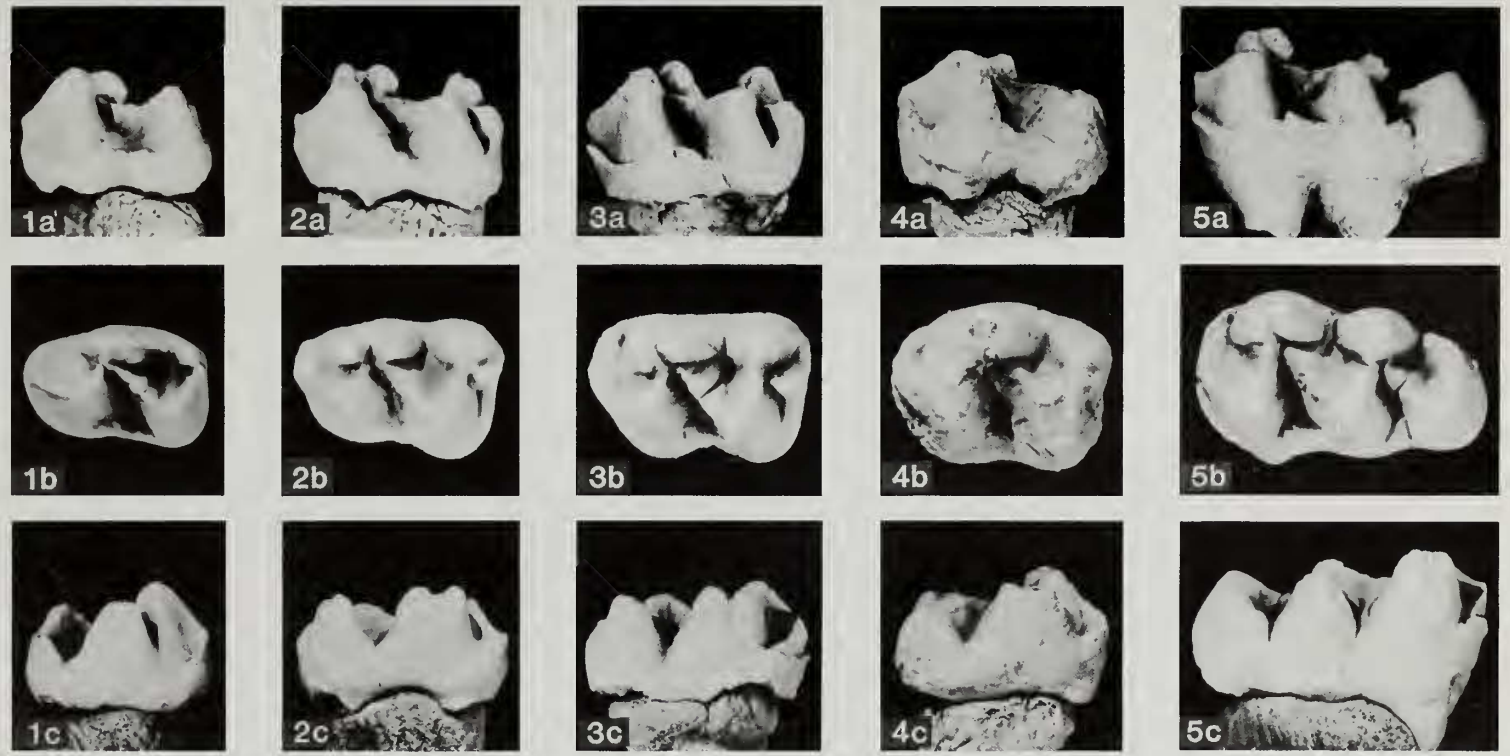
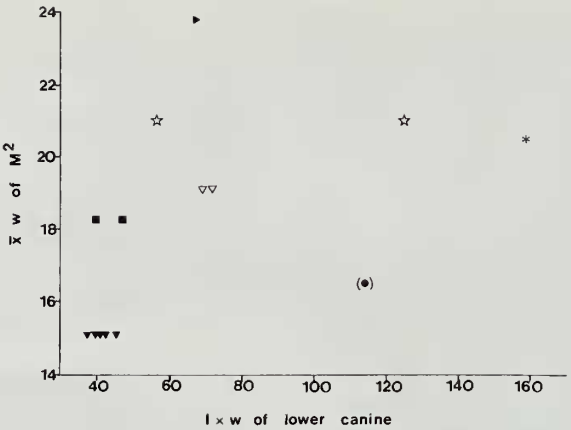


Plate 23 Light macrographs of lower cheek teeth of *Lophiotherium siderolithicum* (Pictet) from Creechbarrow, × 4. a, buccal, b, occlusal and c, lingual views. Fig. 1a–c, left DP_2 (M35585). Fig. 2a–c, left DP_3 (M37447). Fig. 3a–c, right DP_4 (reversed) (M37452). Fig. 4a–c, left P_4 (M37430). Fig. 5a–c, left M_3 (M37438). See p. 347.



Text-figure 45 Scatter diagram of length × width of lower canine against mean width of M^2 of *Plagiolophus* and *Paraplagiolophus*. Measurements in millimetres. ■ = *Plagiolophus annectens* (Owen) from Hordle Cliff; ▼ = *P. minor* (Cuvier) from La Débruge; ▶ = *P. fraasi* Meyer from the Phosphorites du Quercy; ▽ = *P.* sp. from Egerkingen γ; ∗ = *P. curtisi curtisi* sp. & subsp. nov. from Barton Cliff; ● = *P. curtisi creechensis* subsp. nov. from Creechbarrow; ☆ = *Paraplagiolophus codiciensis* (Gaudry) from Jumencourt (Upper Calcaire Grossier).

shallow between diastemata; frontal region flat with supraorbital rims and postorbital processes thin and horizontal; ascending mandibular ramus posteriorly expanded. (Note that the non-dental characters are only known for the nominate subspecies. Dental characters are numbered for later discussion).

Plagiolophus curtisi curtisi subsp. nov.

(Pl. 24, figs 1–2; Pl. 25; Pl. 26, fig. 4; Text-figs 45, 46, 47A, 48A–C, 49B, 50C–D, 51; Table 28)

v. *1972* *Plagiolophus cartailhaci* Stehlin; Hooker: 180–182.
v. *1980* *Plagiolophus* sp. 2; Hooker & Insole: 42.

NAME. After Mr R. J. Curtis, who found the only known specimens.

HOLOTYPE. Very fragmentary associated cranium and mandible (M26176) consisting of 15 non-fitting pieces: palatal fragment with ventral parts of canine alveoli, root and alveoli of left P^1 and mesial part of lingual root of left P^2; left maxillary fragment with distal root parts of P^2 and P^3–M^3 with crowns; right maxillary fragment with M^{1-3} and part of orbital floor; left and right glenoid regions; fragment of left frontal; mandibular symphysis with roots of right I_1–C and left I_{1-2} and C (right C with fragment of crown); left horizontal mandibular fragment, with distal root of P_3, P_4 and M_2 with crown, roots of M_1; talonid and hypoconulid of left M_3; fragment of left ascending ramus; right horizontal mandibular fragment with distal root of P_4 and M_{1-3} with crowns; fragment of right ascending ramus; fragment of right coronid process; right mandibular condyle; and an undetermined bone fragment. The buccal surfaces of many of the teeth have been eroded, presumably following exposure in the field.

PARATYPE. Right M^3 (M26238).

TYPE HORIZON AND LOCALITY. Proximity of junction of Beds D and E, Barton Clay Formation, Barton Cliff at Barton-on-Sea. From the wave-washed lower part of the cliff at about SZ 236928.

DOUBTFULLY REFERRED MATERIAL. Proximal half of right radius (M34864) from the Barton Clay Formation, Barton Cliff, not *in situ*, but preservation suggesting derivation from around Bed E.

DIAGNOSIS. 1, large (M^2 length 16·5 mm); 2, P^{3-4} protocones mesiodistally elongated; 3, upper molar metaloph without metaconule; 4, subterminal metastyle present.

Table 28 Length (l) and maximum width (w) measurements of *Plagiolophus curtisi* from Creechbarrow and Barton. Measurements in millimetres.

No.	Tooth	l	w	No.	Tooth	l	w
M36181	C^1	(10·7)	–	M36181	C_1	12·0	(9·5)
M37473	C^1	9·3	7·3	M26176	C_1	14·8	10·8
M36181	P^2	6·6	9·8	M36181	P_2	8·5	5·3
M37474	P^2	7·0	9·4	M37484	P_2	–	4·1
M37475	P^2	7·3	–	M36181	P_3	8·6	6·8
M36181	P^3	7·9	12·3	M36182	P_3	7·0	5·0
M37476	P^3	8·3	–	M37485	P_3	7·6	5·4
M26176	P^3	10·5	(13·0)	M36181	P_4	9·9	8·1
M36181	P^4	9·3	14·3	M26176	P_4	12·0	(9·0)
M37479	P^4	(9·4)	–	M36181	M_1	(11·5)	7·9
M26176	P^4	12·3	(15·7)	M26176	M_1	14·3	(9·4)
M36181	M^1	10·3	(15·7)	M36181	M_2	13·0	9·4
M26176	M^1	14·4	(19·5)	M26176	M_2	15·4	11·2
M36181	M^2	13·0	16·5	M37486	$M_{1/2}$	10·7	7·4
M26176	M^2	16·5	(20·2)	M37487	$M_{1/2}$	–	7·9
M36181	M^3	18·7	18·2	M36181	M_3	20·0	8·9
M26176	M^3	23·9	20·3	M37709	M_3	–	8·7
M26238	M^3	20·0	20·6	M26176	M_3	23·3	10·4

DESCRIPTION. *Canines*: The remains of the posteroventral alveolar walls of the upper canines indicate massive roots, once extending at least to the level of P^1 (Pl. 24, figs 1a, d). Viewed dorsally they are parallel and laterally they are at an angle of 20–30° to the diastematal ridges. X-rays of an *in situ* upper canine of *P. fraasi* (M1880) show a corresponding angle of *c.* 40° (Pl. 24, fig. 3). Judged from the muzzle shape, the root apices must converge posterodorsally in this and other species of the genus.

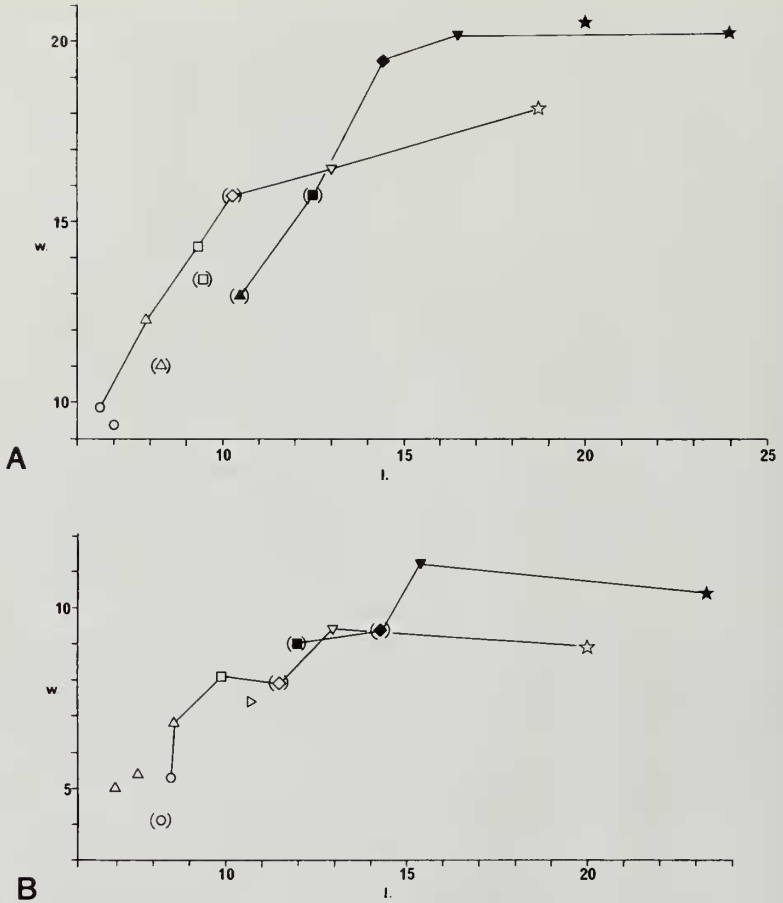
The lower canines of M26176 have similar size and orientation to the uppers but lie closer together; the roots extend to the posterior limit of the symphysis (Pl. 26, fig. 4). X-rays of *P. annectens* and *P. minor* show short convergent roots which terminate posteriorly well in front of the end of the symphysis, despite slight age variation (Pl. 26, figs 2–3). Symphysial shape in the other species indicates similarity to *P. annectens*.

Canine size is compared in Text-fig. 45 with that of other *Plagiolophus* species, in which they are always relatively smaller. The possibility of sexual dimorphism in this feature must be considered (see Stehlin 1905*a*: 330; Depéret 1917: 46). Slight bimodality has been demonstrated for one species of *Palaeotherium* (Franzen 1968: 133) but a similar exercise has not been attempted for *Plagiolophus*. The examination of much material in various European museums has not shown any individuals with canines as large as those of M26176. Their occurrence in more than one individual at Creechbarrow is further support for canine size as a taxonomic character, whether or not it may eventually turn out to be dimorphic in this species.

Upper premolars: P^1 is interpreted as having had three roots, being represented now by a lingual root, a distobuccal alveolus and an eroded or partially resorbed mesiobuccal alveolus. The tooth may thus have been very worn and about to fall out.

The roots of P^2 in spanning two non-fitting bone fragments guide reconstruction in this area (see Text-fig. 51, p. 366).

On P^3 there is evidence of a metacone, despite the buccal erosion and heavy wear, since there appear to be two lingual bulges from the remains of the ectoloph and the paracone has a mesial position. The paraconule is distinct on the protoloph. The complete edges of the tooth have a continuous cingulum, which distally forms a high ridge. Heavy wear has fused this ridge to the metaloph and ectoloph but it is still separated from the protocone by a valley. The metaloph is fused distally to the ectoloph whilst mesially it is terminated by minor buccal and lingual crests, the last joining the protocone.



Text-figure 46 Scatter diagram of length (l) against width (w) of (A) upper and (B) lower cheek teeth of *Plagiolophus curtisi curtisi* sp. & subsp. nov. from Barton Cliff (solid symbols), and *P. curtisi creechensis* subsp. nov. from Creechbarrow (outline symbols). Measurements in millimetres. ○ = $P\frac{2}{2}$; △ = $P\frac{3}{3}$; □ = $P\frac{4}{4}$; ◇ = $M\frac{1}{1}$; ▽ = $M\frac{2}{2}$; ☆ = $M\frac{3}{3}$; ▷ = $M_{1/2}$. Lines join teeth of one individual.

P^4 is similar to P^3 but the paracone and metacone seem better separated. The metaloph has similar mesial crests to P^3 and bends at its distal end to fuse with the protocone. The resultant hook-shaped structure ('crochet' of Stehlin, 1904*a*: 461) resembles that of P^4 of *P. cartailhaci* (Stehlin 1904*a*: pl. 12, fig. 1) and was the main reason for earlier misidentification of M26176 as *P. cartailhaci* (Hooker 1972). The 'crochet' also occurs in some individuals of *P. annectens* (Depéret 1917: pl. 9, fig. 2; Remy 1967: text-fig. 4). The cingulum is interrupted lingually.

Upper molars: In M26176, the protocone and paraconule are fused by wear on M^1 but not on the less worn M^{2-3}. On the even less worn M26238, the paraconule is connected to the protocone. The paraconule protrudes less distally from the protoloph than in higher-crowned species like *P. annectens*. The buccal cingulum in M26176 is very weak (where this region is not eroded away), but it is not certain whether or not this constitutes individual variation; M26238 is also eroded here.

On the M^3s of both individuals (Pl. 24, figs 1b–c, 2a–b), the subterminal metastyle is absent from the basal half of the buccal wall, but a detached, more distal basal swelling could also be construed as part of the metastyle. In M26176, the hypostylar or distal cingular region is relatively expanded in length and height. It is formed from two curved crests, from the distal

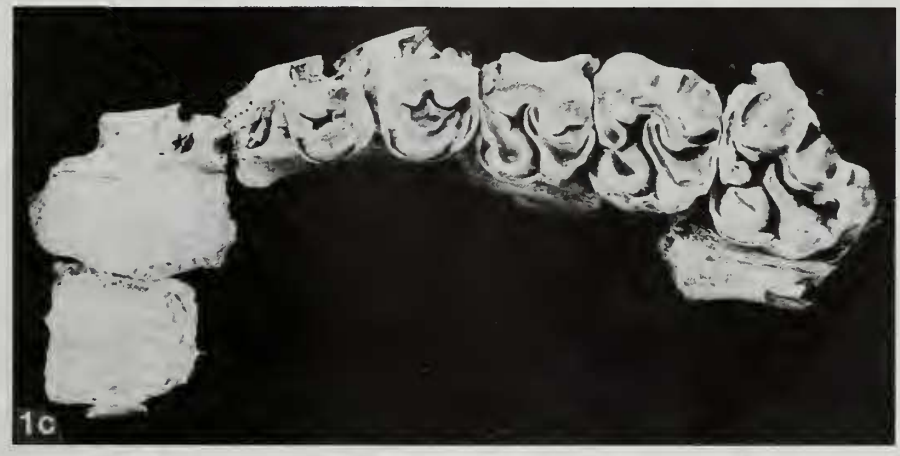
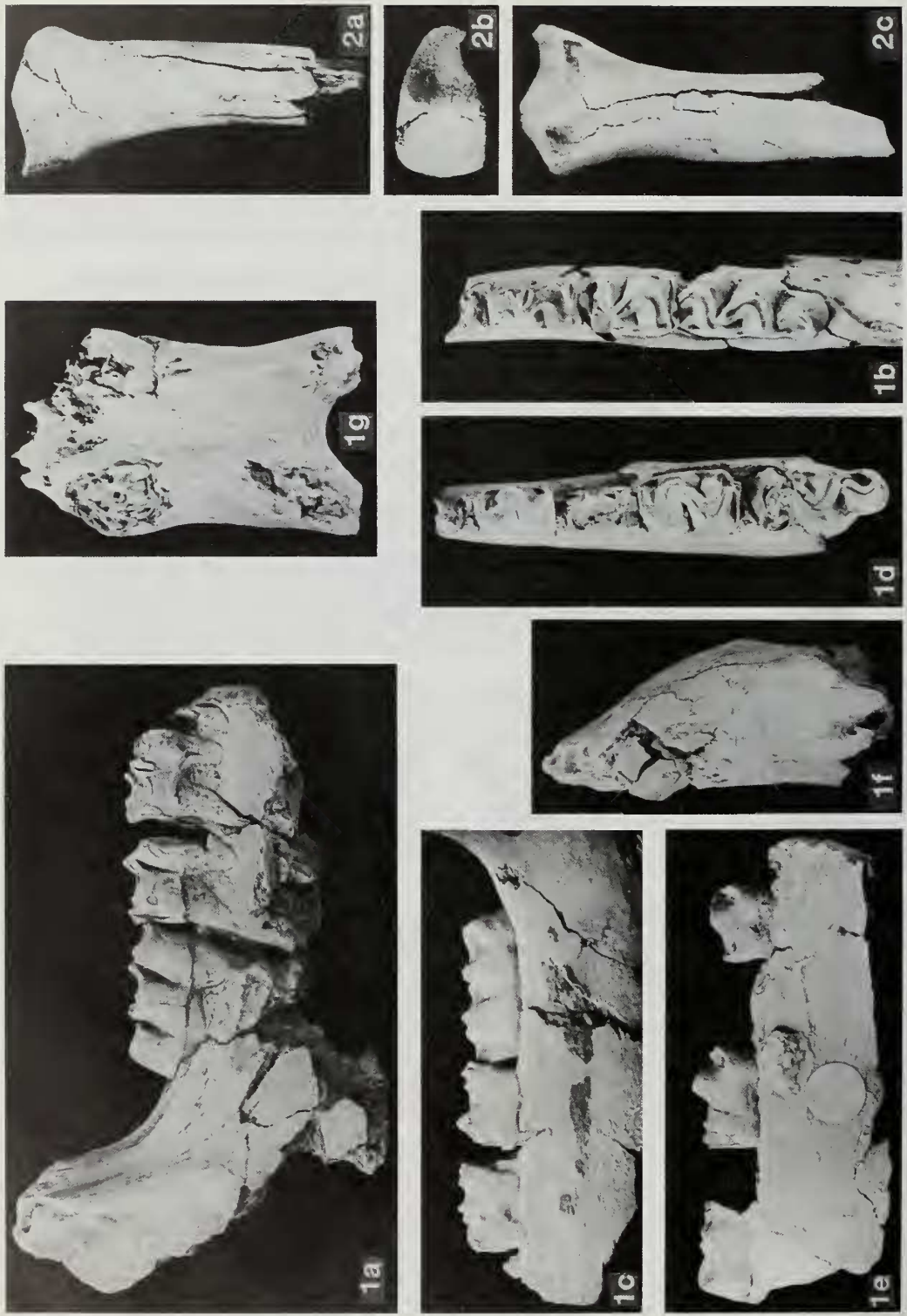


Plate 24 Light macrographs and x-ray of upper teeth and cranial fragments of *Plagiolophus*, × 1.

Figs 1–2 *Plagiolophus curtisi curtisi* sp. & subsp. nov. from Barton. Fig. 1a–f, **holotype** (M26176): a, left dorsolateral view of palatal fragment; b, buccal view of left P^3–M^3; c, ventral view of palatal fragment and occlusal view of P^3–M^3; d, dorsal view of palatal fragment; e, dorsal view of left frontal fragment; f, ventral view of left frontal fragment. Fig. 2a, b, buccal (a) and occlusal (b) views of right M^3 (M26238). See p. 356.

Fig. 3 *Plagiolophus fraasi* Meyer from Caylux: side view x-ray of right maxillary–premaxillary fragment with canine (M1673).


2a
2b
2c
1g
1b
1d
1a
1f
1c
1e

ends of the ectoloph and hypocone, which meet in the middle of the distal tooth margin; the ectolophal part projects distally more than the hypoconal part. M26238 is slightly less expanded distally than M26176, especially from the ectoloph, the distal hypoconal crest is lower and the two crests meet at a V-shaped distal concavity. Potential variation in this subspecies can only be observed on these two M^3s, and appears to be restricted to height of connection of paraconule to protocone (probably affecting the other molars as well) and degree of distal expansion. The curious subterminal metastyle is likely to be at least of common occurrence, if not a constant character. Too few specimens are known to test constancy of size but both M^3s are very close and the other teeth of M26176 are all larger than any of their equivalents (mainly different individuals) from Creechbarrow.

Lower premolars: The only remnant of P_3, the distal root, is as broad as on the Creechbarrow P_3s where a hypoconid is present (Pl. 25, fig. 1d). The P_3 of *P. annectens*, which lacks a hypoconid, has a small peg-like distal root. Moreover, the presence of a P_3 hypoconid in M26176 can be extrapolated from the presence of a P^3 metacone. P_4 is as far as can be observed typical for the genus.

Lower molars: Right M_1 is missing the mesial half of its lingual margin and is buccally eroded; both M_2s are better preserved and similar to M_1; right M_3 is complete. The metaconid and entoconid (and hypoconulid in M_3) have broad bases as seen lingually and tend to reduce the depth of the valleys enclosed by the first and second (and third on M_3) crescents (Pl. 25, fig. 1c, e). The effect is to give the teeth a robust appearance. Some specimens of other species of the genus have slight development of this feature, but its occurrence also in the Creechbarrow lower molars suggests that it might represent more than just individual variation in this case.

Skull: What remain of the side walls of the maxillae diverge dorsolaterally from the diastematal ridges more than in other species of the genus, presumably to house the large parallel upper canine roots. Only the left postcanine diastema is complete posteriorly and neither is complete anteriorly. The maximum measurable length is 14·4 mm, but they are estimated to have been at least 23·0 mm long, thus similar in relative length to those of *P. annectens*. The internal nares extend anteriorly to between the level of M^2 and M^3.

The infraorbital foramen is above the junction of P^3 and P^4, in contrast to *P. annectens* and *P. minor* where it is above the middle of P^4, and to *P. cartailhaci* and *P. fraasi* where it is above the anterior half of M^1. It migrates posteriorly in ontogeny, but moves little (less than the length of P^4) after the permanent premolars have erupted, a stage passed by the specimens considered here.

Immediately behind the infraorbital foramen there is part of a preorbital fossa (Pl. 24, fig. 1b). These may be of two kinds in the other equoid family, the Equidae (Gregory 1920): an upper ('lacrymal') and a lower ('malar'), which sometimes merge to form one. Its preserved anteroventral edge is sharp and extends posteriorly for the length of P^4 in the 'malar' region, but its dorsal extent is unknown. Gregory (1920: 282) stated that neither *Palaeotherium* nor *Paloplotherium* (= *Plagiolophus*) shows pronounced preorbital fossae, but, in addition to M26176, a maxilla of *P. fraasi* (M14734) from the Bembridge Marls of Bembridge shows part of a 'malar' fossa (Text-fig. 47B). Shallow preorbital depressions in *P. annectens* (Owen 1848*a*: pl. 3, fig. 1) and another *P. fraasi* specimen (M1733) from the Phosphorites du Quercy reach dorsally to the nasals, covering both 'malar' and 'lacrymal' regions, but like modern *Equus* lack sharp rims

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Plate 25 Light macrographs of lower teeth, jaw fragments and radius of *Plagiolophus*, × 1.

Fig. 1a–g *Plagiolophus curtisi curtisi* sp. & subsp. nov. from Barton, **holotype** (M26176): left mandibular ramus with P_4, M_{2-3} in occlusal (d) and lingual (e) views; right mandibular ramus with M_{1-3} in buccal (a), occlusal (b) and lingual (c) views; mandibular symphysis in right lateral (f) and dorsal (g) views. See p. 356.

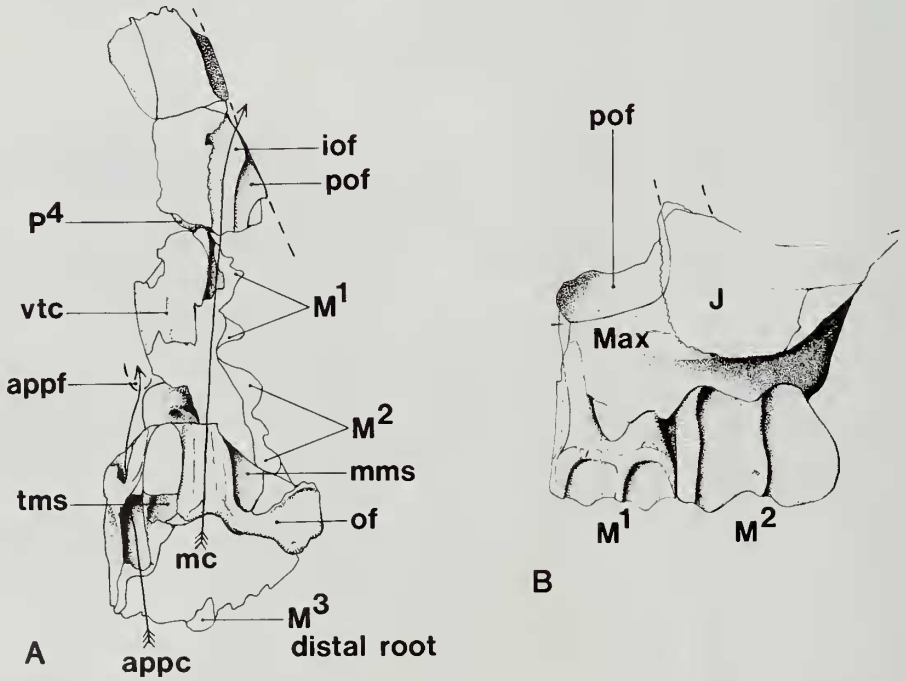
Fig. 2a–c ?*Plagiolophus* sp. indet. Proximal half of right radius from Barton (M34864). Views are anterior (a), proximal (b) and posterior (c). See p. 364.

(Gregory 1920: pl. 18). The apparent individual nature of this fossa in *Plagiolophus* contrasts with the hipparionine equids, where it is considered a generic character (Woodburne & Bernor 1980).

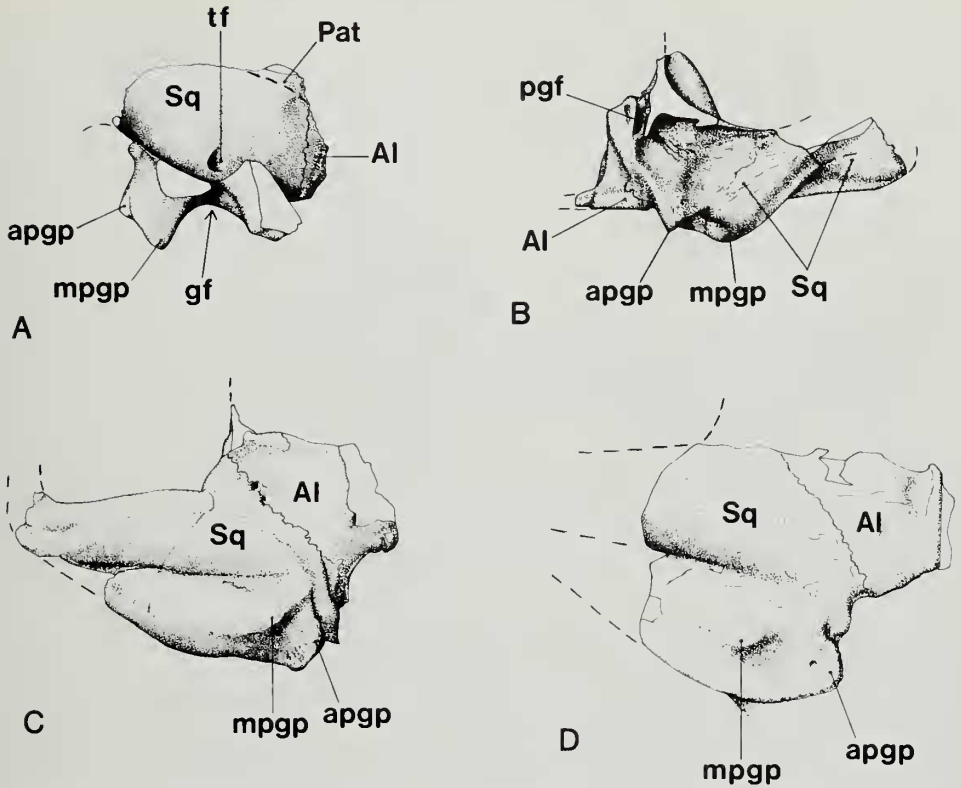
The cranial roof is known only from a fragment interpreted as part of the left frontal (Pl. 24, figs 1e–f; Text-fig. 49B). Its dorsal surface was flat, the supraorbital rim thin and the postorbital process thin and horizontal, in contrast to other species where it is gently domed with the supraorbital rims thick and the postorbital processes strongly downturned (e.g. Text-fig. 49A).

The leading edge of the orbit appears to have extended forward to a point above the junction of M^1 and M^2, further forward than in other species: M^2 midpoint in *P. annectens* and *P. fraasi* and M^{2-3} junction in *P. cartailhaci*. As for the infraorbital foramen, the orbital position is ontogenetically variable, but the specimens concerned have similarly worn teeth. The orbital floor and adjacent areas are incomplete but show the course of foramina and other structures (Text-fig. 47A). The orbital opening of the maxillary foramen and probably also the anterior postpalatine canal are as in *Pachynolophus lavocati* (Remy 1972: 60–62, text-fig. 9), *P. livinierensis* and *Hyracotherium leporinum* (Savage *et al.* 1965: 44, 46–47, text-fig. 20), *P. annectens* and *P. fraasi*.

The squamosal is perforated by a temporal canal, opening posteriorly at the postglenoid foramen and anteriorly at the temporal foramen (Text-fig. 48). The glenoid region differs from that of *P. fraasi* as follows: the main postglenoid process is slightly more prominent but less posteriorly expanded; and the smaller posteromedial accessory process is shorter but more sharply differentiated from the main process. Individual variation in these features is unknown.



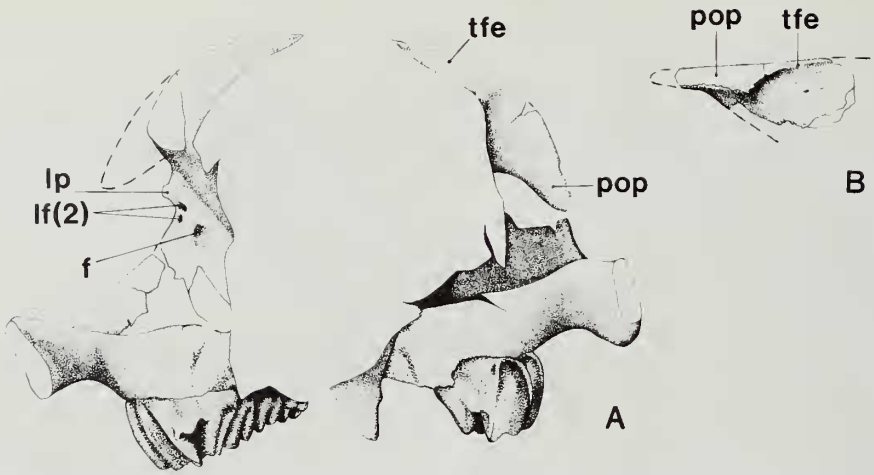
Text-figure 47 A, *Plagiolophus curtisi curtisi* sp. & subsp. nov., **holotype** M26176 from Barton Cliff. Dorsal view of maxillary fragment (incorporating part of the palatine) drawn as from the right side, consisting of the left maxillary fragment from P^4 forwards (reversed) and right maxillary fragment from M^1 backwards. Abbreviations: appc = anterior postpalatine canal; mms = maxillary sinus (main part), tms = maxillary sinus (turbinate part); vtc = ventral turbinate crest; for other abbreviations see Text-fig. 51, p. 366. × 1. B, *Plagiolophus fraasi* Meyer, M14734 from the Bembridge Marls of Bembridge. Lateral view of right maxillary fragment (reversed). × 1.



Text-figure 48 *Plagiolophus*, glenoid region. A–C, **holotype** of *Plagiolophus curtisi curtisi* sp. & subsp. nov. (M26176) from Barton Cliff. D, *P. fraasi* Meyer (M1733) from the Phosphorites du Quercy. A, lateral view of right glenoid region; B, posterior view of right glenoid region; C, ventral view shown as right glenoid region, but composite of right and left; D, ventral view of left glenoid region (reversed). Abbreviations: Al = alisphenoid; apgp = accessory postglenoid process; gf = glenoid fossa; mpgp = main postglenoid process; Pat = parietal; pgf = postglenoid foramen; Sq = squamosal; tf = temporal foramen. All × 1.

The mandibular symphysis is massive for housing the canine roots. Its ventral edge is angled anterodorsally below a point just behind the emergence of the canines. In contrast the small symphyses of other species have an even, anterior tapering, shape. The symphysis in M26176 terminates an unknown distance in front of the premolar row; in *P. annectens* it is just in front of P_2. The maximum length measurable on the lower diastemata of M26176 is 23·0 mm, the same as that estimated for the complete upper diastema. As there was apparently no tooth immediately following the breakage of the lower diastema, P_1 was probably absent, P_2 beginning the row behind the main mental foramen. In dorsal view the symphysis is only slightly concave laterally and the diastematal ridges are almost straight. In other species it is laterally more deeply concave and so are the ridges. Like the palate, the interdiastematal symphysial concavity is shallower in *P. curtisi* than in other species of *Plagiolophus*.

The anteromedial edge of the ascending ramus forms an acutely angled ridge because the masseteric ridge lies posterolateral to it. This contrasts with other species where both ridges normally lie side by side and are weaker and more rounded. The curvature of the posterior edge of the coronoid process indicates a more gentle slope towards the condyle than in other species. The same character in a specimen of *Paraplagiolophus codiciensis* (MNHN, labelled 'M. Guérin Cat. 20') is associated with a more posteriorly expanded angular region and a lower, less recurved coronoid process. The condyle is similar to that of *P. annectens* but is thicker and



Text-figure 49 *Plagiolophus*, posterior cranial views. A, syntype of *P. annectens* (Owen) (29729) from Hordle Cliff. B, **holotype** of *P. curtisi curtisi* sp. & subsp. nov. (M26176) from Barton Cliff. Abbreviations: f = fossa; lf = lacrymal foramina; lp = lacrymal process; pop = postorbital process; tfe = edge of temporal fossa. × 1.

has a sharp anterolateral ridge. Posteroventrally the beginning of the angular edge is orientated more like *P. codiciensis* than a species of *Plagiolophus* (Text-fig. 50).

Tentatively referred radius: The proximal articulation measures 14·0 mm anteroposteriorly and 23·3 mm mediolaterally. Both are probably slight underestimates as the bone is somewhat eroded anteriorly and laterally. The maximum length of the incomplete shaft is 56·5 mm (Pl. 25, fig. 2). It is very similar in size and morphology to radii of *P. annectens* from Hordle Cliff and La Débruge and in morphology to those of *P. minor* from La Débruge. All species of *Palaeotherium* examined in comparison had a medially bowed radius, resulting in the proximal articulation being slightly oblique, compared to the nearly straight *P. annectens* radius. *Palaeotherium* radii also tend to be shorter and broader but this feature cannot be observed on M34864.

Plagiolophus curtisi creechensis subsp. nov.
(Pl. 26, fig. 1; Text-figs 45, 46, 52C–D, 53; Table 28)

v. *1977b Plagiolophus* aff. sp. nov.; Hooker: 141.
v. *1980 Plagiolophus* sp. 1; Hooker & Insole: 42.

Name. From the tithing of Creech in the parish of Church Knowle, overlooked by Creechbarrow.

Holotype. Associated upper and lower dentitions (M36181): left C^1, P^2–M^3; right P^2–M^3; left I_2?, C_1, P_2–M_3; right C_1, P_4–M_3. Numerous indeterminate fragments, probably mainly from the jaws, are likely also to be associated.

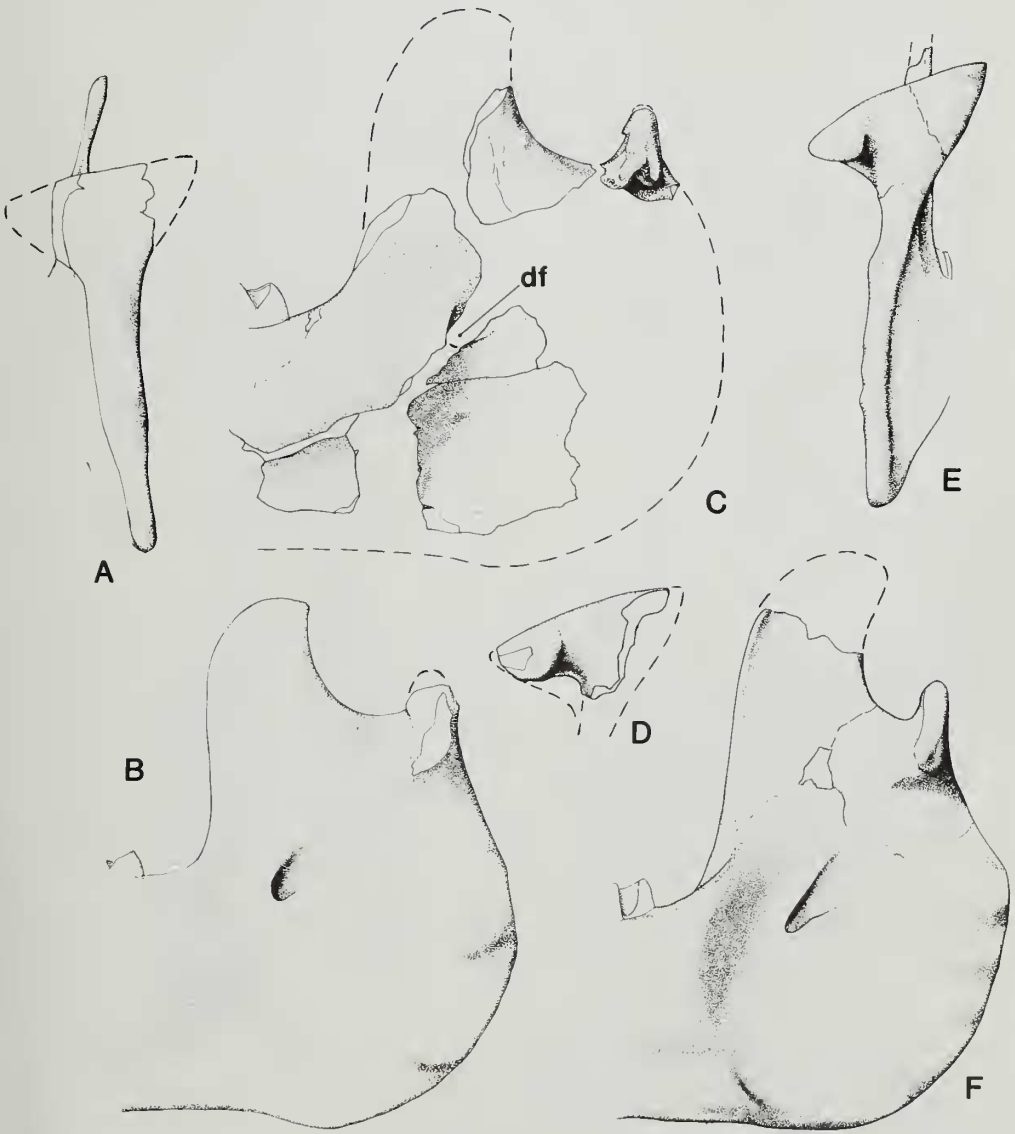
Paratypes. (18): Upper canine (M37473); two P^2s (M37474–5); two or three P^3s (M37476–7, ?M37478); P^4 (M37479); four fragmentary upper molars, mainly if not all $M^{1/2}$s (M37480–3); two P_2s (M36182, M37484); P_3 (M37485); two $M_{1/2}$s (M37486–7); M_3 (M37709); lower molar trigonid fragment (M37488).

Doubtfully referred material. Two incisors (M37489–90); left petrosal (M37491).

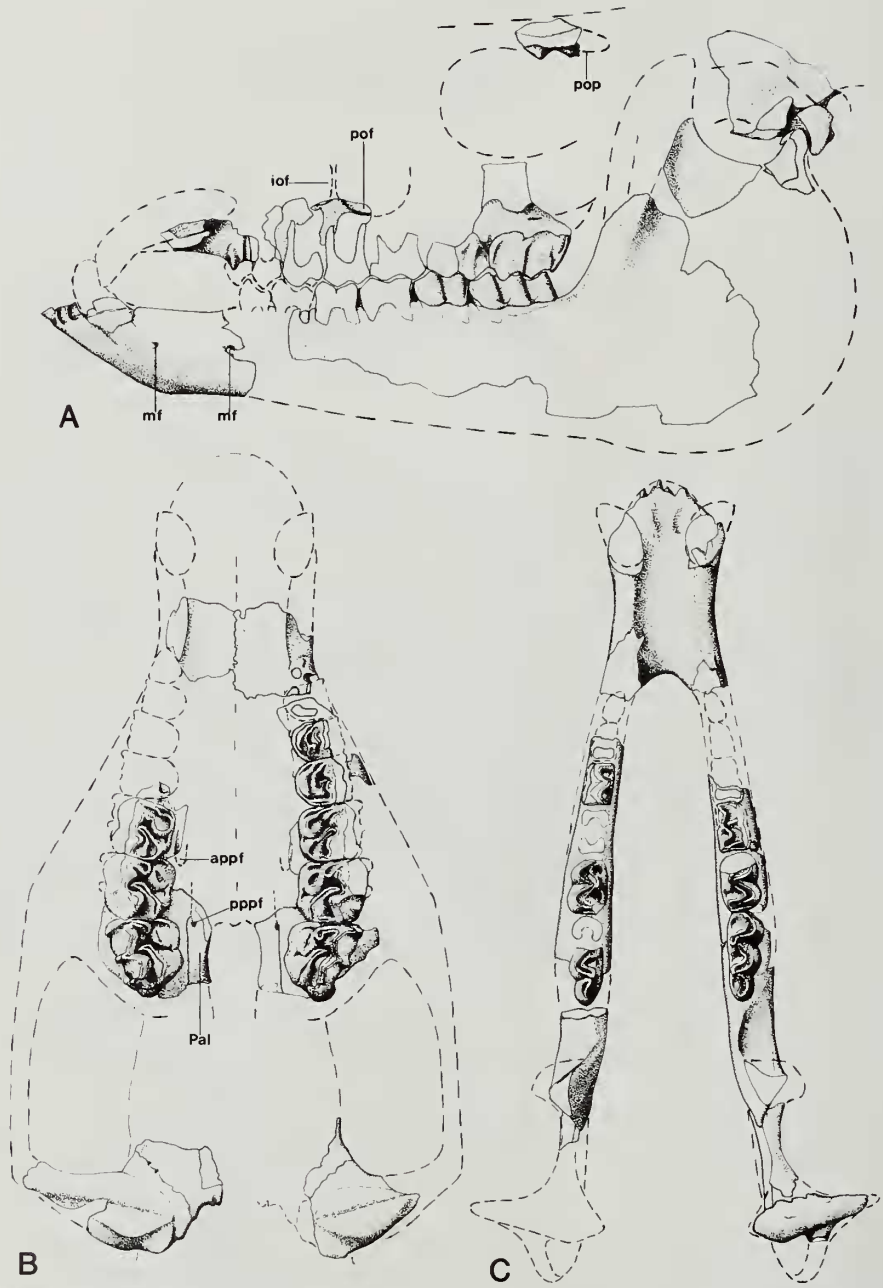
Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Diagnosis. 1, small (M^2 length 13·0 mm); 2, P^{3-4} protocones conical; 3, small metaconule on upper molar metaloph; 4, no accessory subterminal metastyle.

DESCRIPTION. *Canines*: It has been shown above that the canines of M26176 are not splayed like those of other species of *Plagiolophus* but have essentially parallel orientation and the uppers are more laterally spaced than the lowers. Because of ectental cheek tooth motion in *Plagiolophus*, the striations produced on the transverse-vertical facets of the canines in the 'splayed' species run longitudinally on the uppers and transversely on the lowers (Text-fig.



Text-figure 50 Ascending mandibular rami (shown as right) of *Plagiolophus* and *Paraplagiolophus*, × 0·75. A–B, *Paraplagiolophus codiciensis* (Gaudry) (MNHN unnumbered) from Jumencourt (Upper Calcaire Grossier); posterior and medial views respectively of left ascending ramus (reversed). C–D, *Plagiolophus curtisi curtisi* sp. & subsp. nov., **holotype** (M26176) from Barton Cliff; medial and posterior (condyle only) views respectively of fragmentary right ascending ramus. E–F, *Plagiolophus annectens* (Owen) (28229, Bravard Cat. no. G148) from La Débruge; posterior and medial views respectively of left ascending ramus (reversed). Abbreviation: df = dental foramen.



Text-figure 51 *Plagiolophus curtisi curtisi* sp. & subsp. nov., holotype (M26176) from Barton Cliff. Partial reconstruction of skull, × 0·5. A, left lateral view of left and right composite. B, ventral view of cranium. C, dorsal view of mandible. Abbreviations: appf = anterior postpalatine foramen; iof = infraorbital foramen; mf = mental foramen; Pal = palatine; pof = preorbital fossa; pop = postorbital process; pppf = posterior postpalatine foramen.

52A–B). Observation of striations on *P. curtisi creechensis* should confirm whether or not the canine angle was as in *P. curtisi curtisi* or as in the other species. Unfortunately no striations are preserved, although parts of the facets remain on some of the incomplete canines. The apical half of the left lower canine of the holotype preserves almost all the facet, including part of its basal margin towards the lingual side. Here the facet margin slopes buccobasally, leaving a lingual ridge unworn at the same crown level. If wear had been completely transverse, this ridge would almost certainly have sustained wear (Text-fig. 52C–D). It is thus tentatively concluded that wear was oblique and that the canines in the lower jaw at least had approximately parallel orientation as in *P. curtisi curtisi.*

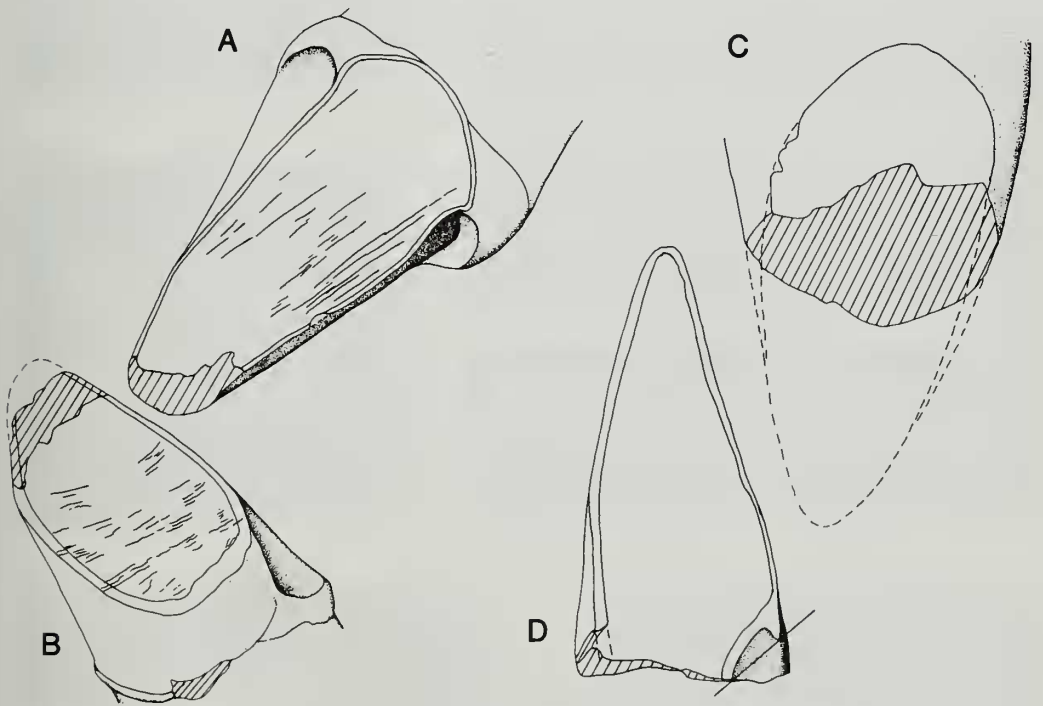
The lower canines are almost as large as those of M26176, whilst an upper (M37473) fits reasonably well in the remains of the upper alveoli of M26176.

Upper premolars: P^1 is known to have existed from mesial interstitial facets on the P^2s.

Complete P^2s from two individuals (M36181, M37474) show the metacone and mesostyle to be absent, but the paraconule to be a distinct cusp. On one the metaconule is joined to the distal cingulum, on the other it is isolated.

The only complete P^3 is the left one of the holotype. It has equal-sized paracone and metacone lying close together with the paracone bulging lingually more than the metacone, as in M26176. The large metaconule is linked by a narrow crest (missing on the right holotype P^3) to the distal cingulum. There is no mesostyle.

There are two individuals to show variation in P^4. At similar wear stages, M36181 shows the metaconule joined to the protocone in a complete 'crochet' structure as in M26176, whereas in



Text-figure 52 Occlusal views of canines in *Plagiolophus* showing orientations at beginning of buccal phase. A–B, *P. fraasi* Meyer from the Phosphorites du Quercy; C–D, *P. curtisi creechensis* subsp. nov. from Creechbarrow. A, Right upper canine (M1673); B, left lower canine (M1750); C, ?left upper canine (reversed) (M37473); D, left lower canine. Wear facets of A and B show striations indicating direction of motion; oblique line delimiting lower edge of facet in D indicates suggested maximum transverse angle of mastication. Oblique hatching indicates broken surfaces. × 5.

1a

1b

1c

1d

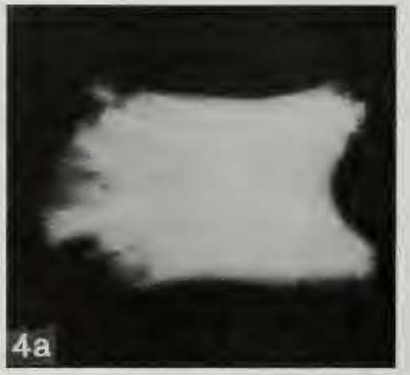
1e

1f

2a

2b

3


4a

4b

M37479 the distal end is bent lingually at right angles, separated from the protocone, and a small bulge crosses the valley almost meeting the distal cingulum. The mesial end of the metaloph is simple in both specimens. M36181 is the only individual complete enough to show that, although a mesostyle is absent, a very faint ridge is present at the base and top of the ectoloph between the paracone and metacone.

The cingulum is interrupted lingually on P^{2-4}, but the contrast with *P. curtisi curtisi* is likely to be of an individual nature.

Upper molars: Only the holotype shows distinguishing characters. The buccal cingulum is interrupted opposite the metacone on M^3, otherwise it is complete although not very strong. Degree of separation of the paraconule from the protocone is very similar to M26176. The degree of distal expansion of M^3 is intermediate between that described above for M26176 and M26238, but similar to both in style. The subterminal metastyle is absent from this tooth in M36181, but the more distal basal swelling is present.

Lower premolars: Available P_2s have no mesial interstitial facet, so it is concluded that P_1 was absent.

In three P_2s there is slight variation in the size of the metaconid. It ranges from insignificant and style-like to three-quarters the height of the protoconid. There is a low, almost longitudinal metalophid which has a slight lingual bend at its distal end, the only recognizeable homologue of the hypoconid. The buccal cingulum varies from weak and interrupted to completely missing.

The hypoconid is smaller on P_3 (M36181) than on P_4 and the whole talonid is much lower and narrower than the trigonid. The small size of the talonid corresponds to the proximity of the paracone and metacone of P^3 with which it occludes. Because of disto-occlusal flaring, the hypolophid of M37485 has been almost entircly removed by heavy wear.

On the holotype left P_4 the talonid is slightly wider than, and nearly as high as, the trigonid. The latter is less open than on P_3, being more like that of the molars but with a weaker paralophid.

Lower molars: The shallowing of the valleys already mentioned under *P. curtisi curtisi* is hardly visible on M36181, but it is present in a curious form on an M_3 (M37709) which has the hypoconulid and part of the hypolophid broken away. Lying in the valley enclosed by the second crescent there is a transverse rib which merges lingually with a mesial extension of the base of the entoconid. Apart from slightly lower crown height, the lower molars are otherwise similar to those of *P. annectens*.

Tentatively referred petrosal: The identification of this isolated bone with *P. curtisi creechensis* should be considered as no more than very tentative. The only perissodactyl genus in the Creechbarrow fauna the right size is *Plagiolophus*, but as so few published accounts of the ear region of European perissodactyls exist, the taxonomic relevance of morphological differences cannot easily be assessed.

M37491 has been compared with an as yet undescribed petrosal *in situ* in a cranium of *P. fraasi* (M1733) from the Phosphorites du Quercy, two isolated petrosals from the Hordle Cliff

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Plate 26 Light macrographs of cheek teeth and x-rays of symphyses of *Plagiolophus*, × 1.

Fig. 1a–f *Plagiolophus curtisi creechensis* sp. & subsp. nov., **holotype** (M36181) from Creechbarrow. a, buccal view of left P^2–M^3; b, occlusal view of left P^2–M^3; c, occlusal view of right P^2–M^3; d, buccal view of left P_2–M_3; e, occlusal view of left P_2–M_3; f, lingual view of left P_2–M_3; note that hypoconulid lobe is broken on M_3. See p. 364.

Figs 2–3 *Plagiolophus annectens* (Owen) from Hordle Cliff. X-rays of mandibular symphyses. Fig. 2a, b, younger individual (BM(NH) 29730) in dorsal (a) and lateral (b) views. Fig. 3, older individual (BM(NH) 29705) in dorsal view.

Fig. 4a, b *Plagiolophus curtisi curtisi* sp. & subsp. nov., **holotype** from Barton Cliff (M26176). X-ray of mandibular symphysis in (a) dorsal and (b) lateral views. See p. 356.

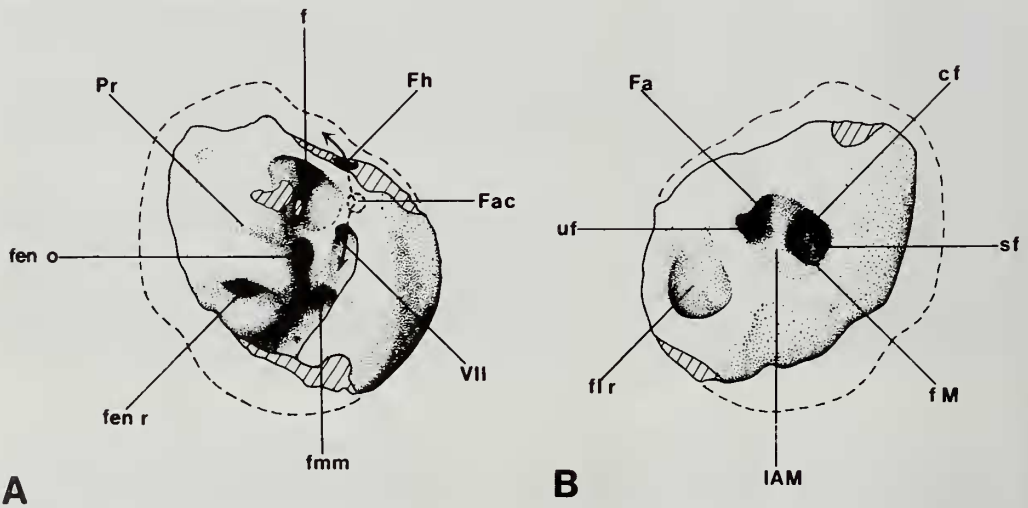
Mammal Bed (R. Gardner private collection) and figures and descriptions of *Pachynolophus livinierensis* Savage, Russell & Louis 1965 (Savage *et al.* 1965: 48, 51–52, text-fig. 22; pl. 1) and *Pachynolophus lavocati* Remy 1972 (Remy 1972: 66–69, text-fig. 11; pl. 4). (Note that Savage *et al.* 1965: pl. 1 shows a right petrosal, not a left as stated).

The specimen is worn and broken but its significant differences from the other petrosals mentioned above will be described. Terminology used here follows Savage *et al.* (1965), MacIntyre (1972) and Remy (1972). Most of the edges of the bone are broken away except for the posterior half of the lateral edge. The main position of the foramina and other structures are indicated in Text-fig. 53.

In ventral view, the basic pattern of the foramina is the same in all the material mentioned but, in contrast to the others, in M37491 there is a facial canal bridge. The Fallopian hiatus is thus more anterior and occurs in an area of marginal breakage. The rim of the fenestra ovalis is also raised and, anteromedially of these two areas, there is left a distinct oval fossa in the area of the sulcus arteriosus promontorii.

On the dorsal surface, the two depressions of the internal auditory meatus have an anterolateral/posteromedial spatial relationship as in M1733. The Fallopian aqueduct is overhung by an anterior lip and is orientated anterodorsally. The utricular fossette occupies all the posterolateral half of the anterolateral depression. The cochlear fossette is large and the saccular fossette posterolateral to it. The foramen of Morgagni is very small and sharp-rimmed and almost vertically perforates the posterolateral wall of the posteromedial depression. Lateral to the internal auditory meatus is the floccular (subarcuate) fossa, which in M1733 and the Hordle Cliff specimens is absent.

Discussion of *P. curtisi*. Characters 6, 7 and 8 of the diagnosis of *P. curtisi* are shared with *P. annectens*, *P. minor* and *P. fraasi* of the Ludian. Characters 3, 4, 5, 12, 17, 18, 19 and 20 are shared with an undescribed species from the late Lutetian of Egerkingen γ. Characters 10, 11 and 15 are intermediate between the two types; so are the proximity of the P^3 paracone and



Text-figure 53 Eroded left petrosal (M37491) from Creechbarrow, possibly belonging to *Plagiolophus curtisi creechensis* subsp. nov. A, ventral view; B, dorsal view. Abbreviations: cf = cochlear fossette; f = unnamed fossa; Fa = Fallopian aqueduct; Fac = Fallopian aqueduct (concealed by facial canal bridge); fen o = fenestra ovalis; fen r = fenestra rotunda; Fh = Fallopian hiatus; flr = floccular recess (subarcuate fossa); fM = foramen of Morgagni; fmm = fossa muscularis minor; IAM = internal auditory meatus; Pr = promontorium; sf = saccular fossette; uf = utricular fossette; VII = facial canal (probable course of VIIth (facial) nerve). Oblique hatching indicates broken surfaces. × 3·3.

metacone and small size of the P_3 hypoconid. Characters 9 and 16 are unique to *P. curtisi*. The characters of the earlier species are considered primitive and those shared by the later species advanced. The intermediate characters fit well with the known Bartonian age of the nominate subspecies, whilst its unique characters suggest that it did not give rise to any other known species.

The presence of P^3 metacone and P_3 hypoconid in this and the undescribed Egerkingen γ species has relevance to an understanding of the affinities of *Plagiolophus*. It supports the derivation of this genus from a low-crowned palaeothere such as *Propalaeotherium* (referred to Equidae by Savage *et al.*, 1965) by increase in crown height. The non-molariform $P\frac{3}{3}$ in advanced *Plagiolophus* can then be regarded as a secondary simplification, rather than as evidence of derivation from a condylarth stock independent of *Hyracotherium* (see Butler, 1952*a*, 1952*b*; Remy, 1967, 1976). Detailed discussion of this question will be covered elsewhere.

When first studying the Creechbarrow and Barton *Plagiolophus* material, three alternative classifications appeared possible: 1, simply to consider all the material as one taxonomic unit at species level, on the basis of the unique characters listed above; 2, to separate the two assemblages as different species on the basis of a few minor characters; or 3, to describe them as one species but giving each assemblage a different subspecific name. The mixing of the assemblages resulting from solution 1 was abandoned as confusing. The small size of the assemblages does not give a clear enough idea of the constancy or variation of the distinguishing characters, so solution 2 was abandoned. The apparently constant size difference between the two assemblages is only slightly less than that which occurs between two closely related sympatric species (*P. annectens* and *P. minor* from La Débruge), so solution 3 was used.

Because both subspecies occur in the same general area (Creechbarrow and Barton are only 32 km apart) and because they have not been found in continental European Bartonian sites (where nevertheless other species of *Plagiolophus* are known), it is logical to consider them as probably stratigraphical subspecies or stages in a single lineage. Of the characters which distinguish the two subspecies, 2 and 3 can be considered primitive in *P. curtisi creechensis* and advanced in *P. curtisi curtisi*, as they are shared with *P.* sp. from Egerkingen γ and *P. annectens* respectively. Character 4 may also be an advanced character for *P. curtisi curtisi*, but it occurs in Auversian *P. cartieri* and not in any of the other species, older or younger. The evidence as a whole suggests a slightly earlier age for the Creechbarrow Limestone than for Barton Clay beds D/E.

Genus ***PALAEOTHERIUM*** Cuvier 1804

TYPE SPECIES. *P. magnum* Cuvier 1804. Première Masse du Gypse, Montmartre, Paris, France.

INCLUDED SPECIES. *P. eocaenum* Gervais 1875, *P. siderolithicum* (Pictet & Humbert 1869) Franzen 1968, *P. lautricense* Stehlin 1904*a*, *P. ruetimeyeri* Stehlin 1904*b*, *P. pomeli* Franzen 1968, *P. castrense* Noulet 1863, *P. medium* Cuvier 1804, *P. crassum* Cuvier 1805, *P. renevieri* Stehlin 1904*b*, *P. muehlbergi* Stehlin 1904*b*, *P. curtum* Cuvier 1812, *P. duvalii* Pomel 1853, *P. crusafonti* Casanovas-Cladellas 1975.

RANGE. Late Lutetian–late Ludian, Europe. See Franzen (1968) for details of horizons and localities of the species.

DIAGNOSIS. See Franzen (1968: 16).

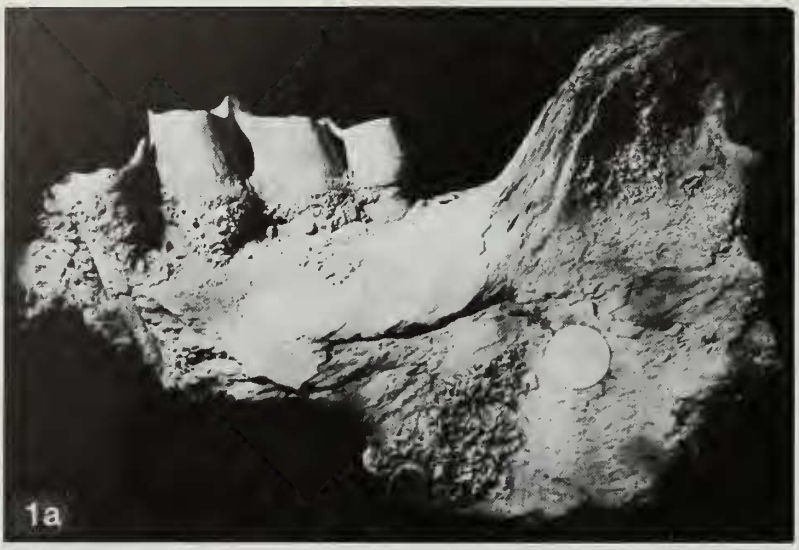
Palaeotherium aff. ?***muehlbergi*** Stehlin 1904*b*
(Pl. 27, fig. 1)

vp. *1980 Palaeotherium* sp.; Hooker & Insole: 43.

LECTOTYPE of *P. muehlbergi*. Left P^{2-3} (Paläontologisches Institut und Museum Zürich no. A/V 242). Ludian fissure filling, Obergösgen, Switzerland.

RANGE of *P. muehlbergi*. Ludian; England, France, Switzerland and West Germany.

DIAGNOSIS of *P. muehlbergi*. See Franzen (1968: 102, 104).


1a

2a

1c

2b

1b

3a

3b

MATERIAL. Left mandibular fragment with distal fragment of M_2 and complete M_3 (M34865).

HORIZON AND LOCALITY. Barton Clay Formation (not *in situ*), on high terrace of Barton Cliff below Naish Estate, near Barton-on-Sea, Hampshire; probably about SZ 223931. The jaw cavity is filled with brown concretionary claystone full of moulds of molluscs, mainly *Turritella*; there is no glauconite. The preservation thus suggests Bed F, which was exposed here at the time of collection in 1976 by Mr I.C. Daniels of Southbourne, Dorset.

DESCRIPTION. The distal width of the remains of M_2 is 16·4 mm. The M_3 is 35·9 mm long; the trigonid width is 15·9 mm, the talonid width is 13·9 mm and the hypoconulid width 10·6 mm.

The M_3 is moderately worn and exact crown height is unknown, but comparison with specimens at similar wear stages indicates that it is fairly low crowned for *Palaeotherium*.

The crescents of M_3 are sharply convex, not blunt and rounded as in *P. magnum*. The hypoconulid lobe is moderately bent and the distal limb is orientated essentially lingually. The extent of wear on the hypoconulid and hypoconid suggests that when unworn the former was not much lower than the latter.

The lingual cingulum is mainly strong but fades between the entoconid and hypoconulid. The buccal cingulum is weak and interrupted at the protoconid, hypoconid and hypoconulid.

COMPARISONS AND DISCUSSION. Eight described species can approach the dimensions of the Barton specimen: *P. pomeli* (Marinesian), *P. ruetimeyeri*, *P. castrense* (late Lutetian–Marinesian), *P. medium*, *P. crassum*, *P. curtum*, *P. renevieri* and *P. muehlbergi* (Ludian).

P. pomeli differs in having higher-crowned teeth and an M1–3 enlargement.

P. medium and *P. crassum* have relatively longer and narrower M_3s with a more continuous buccal cingulum. Moreover, the earlier subspecies, which are closer in age to the Barton specimen, are more different in size than the later ones. These species and *P. curtum* tend to have rounder, less angled crescents. *P. renevieri* is very similar to *P. crassum*.

The remaining three species are very similar to M34865. Both *P. ruetimeyeri* and *P. castrense* have strong continuous buccal cingula, but on *P. muehlbergi* these can be weak and interrupted. *P. muehlbergi* also has characteristically angled crescents but the hypoconulid has a stronger and more mesially directed distal hook.

Of the Marinesian species in the above list, the M_3 from Robiac, attributed to *P.* aff. *ruetimeyeri ruetimeyeri* by Franzen (1968: pl. 4, fig. 8), is closest in size, being only very slightly smaller. This too, though, has a continuous buccal cingulum.

Franzen (1968: 109) considered the possibility that *P. muehlbergi praecursum* Franzen 1968 (the earliest subspecies from Hordle Cliff) could have evolved from *P. ruetimeyeri*, but that the typical and best known assemblage from Egerkingen α was very much older and more primitive than *P. muehlbergi*. He noted that the Robiac specimens did not provide enough information to support this derivation. The Barton specimen demonstrates the presence in the Marinesian of a *P. muehlbergi*-like species, but more complete material would be necessary to test out the above evolutionary hypothesis and to provide a more accurate identification.

Palaeotherium sp. indet.
(Pl. 27, fig. 2)

v. *1979* cf. *Palaeotherium* sp.; Kemp *et al.*: 102.
vp. *1980* *Palaeotherium* sp.; Hooker & Insole: 43.

MATERIAL. Lateral fragment of distal articulation of left humerus (M36491).

Plate 27 Light macrographs of *Palaeotherium* and *Lophiodon*, × 1.

Fig. 1a–c *Palaeotherium* aff. ?*muehlbergi* Stehlin (M34865) from Barton Cliff. Left mandibular fragment with M_3 and distal root of M_2. a, buccal, b, occlusal and c, lingual views. See p. 371.

Fig. 2a, b *Palaeotherium* sp. indet. (M36491) from Elmore. Mediodistal fragment of right humerus. a, anterior and b, distal views. See p. 373.

Fig. 3a, b *Lophiodon* cf. *cuvieri* Filhol (GM.978110–3) from Elmore. Cast (M41977) of left M^3, not sprayed with ammonium chloride. a, occlusal and b, buccal views. See p. 374.

HORIZON AND LOCALITY. Elmore Member, Barton Clay Formation (not *in situ*), foreshore at Elmore, near Lee-on-Solent, Hampshire.

DESCRIPTION. No useful measurements can be taken of this fragment. It compares very well in size and morphology with the relevant part of a complete humerus of *P. magnum stehlini* Depéret 1917 (BM(NH) 29744a) from Hordle Cliff. The characters available, however, do not appear to be species characteristic. The only *Palaeotherium* species of the appropriate size known from the Auversian is *P. castrense*. Specific identification, however, cannot be made, although it seems unlikely that it was conspecific with the specimen from Barton. One must hope that this locality will eventually yield some dental remains of the genus.

Suborder **ANCYLOPODA** Cope 1889
(rank emend. Radinsky 1964) (*sensu* Hooker 1984)

Family **LOPHIODONTIDAE** Gill 1872

TYPE GENUS. *Lophiodon* Cuvier 1822.

REMARKS. The classification by Radinsky (1964: 3–4, 7–9) and Savage *et al.* (1966: 31–35) of *Lophiaspis* Depéret 1910 and *Paleomoropus* Radinsky 1964 in the family Eomoropidae Matthew 1929*a* is followed here, rather than that by Fischer (1964: 62–64, 67, fig. 21; 1977*a*: 917–918), who included them in the Lophiodontidae.

RANGE. Same as *Lophiodon* (q.v.).

Genus ***LOPHIODON*** Cuvier 1822

TYPE SPECIES. *Palaeotherium tapiroides* Cuvier 1812. Middle Lutetian; Bouxwiller, Alsace, France.

INCLUDED SPECIES. *L. remensis* Lemoine 1878, *L. tapirotherium* Desmarest 1822, *L.? buchsowillanum* Desmarest 1822, *L. parisiense* Gervais 1852, *L. cuvieri* Filhol 1888*a*, *L. thomasi* Déperet 1906, *L.? isselense* Fischer 1829, *L. rhinocerodes* Rütimeyer 1862, *L. lautricense* Noulet 1851, *L. sardus* Bosco 1902, *L.? leptorhynchum* Filhol 1888*a*. For additional doubtful species see Fischer (1964: 67). For differing views of species, see Fischer (1964, 1977*a*, 1977*b*), Jaeger (1971) and Sudre (1971).

DISCUSSION. Dedieu (1977, June) placed *L. buchsowillanum* (type species), *L. isselense*, *L. leptorhynchum* and *L. compactus* Astre 1960 (the last raised to species level) in his new genus *Paralophiodon*, which he referred to a new monotypic subfamily Paralophiodontinae of the family Isectolophidae. Fischer (1977*a*, July) placed *L. buchsowillanum* in his new monotypic lophiodontid genus *Rhinocerolophiodon* (thus a junior objective synonym of *Paralophiodon*) and referred *L. leptorhynchum* to *Lophiaspis*. Until more detailed evidence is published, a conservative approach is adopted here.

RANGE. Late Ypresian to Bartonian (Marinesian), Europe and possibly south-west Asia.

DIAGNOSIS. See Fischer (1977*b*: 1129).

Lophiodon cf. ***cuvieri*** Filhol 1888*a*
(Pl. 27, fig. 3)

v. *1980* *Lophiodon* cf. *cuvieri* Filhol; Hooker & Insole: 43.

SYNTYPES of *L. cuvieri*. Cranium and left mandibular ramus. Upper Calcaire Grossier (late Lutetian); Jouy, Marne, France (Filhol 1888*a*: 144–154; pls 14–15; pl. 16, figs 3–5; pl. 17, fig. 5). Neither Schroeder (1916) nor Fischer (1964) were able to find the specimens although they were stated to be in the Sorbonne, Paris by Filhol (1888*a*: 144) and Stehlin (1903: 116).

Lophiodon cuvieri Watelet 1864 is a *nomen nudum*, as this author gave no figures or any information which can be construed as a description or even mention of a single distinguishing feature. The species must therefore take its authorship and date from Filhol (1888*a*).

RANGE of *L. cuvieri*. Early or middle Lutetian, D.D.R.; ?Lutetian, B.R.D. (see Tobien 1961) (*L.* cf. *cuvieri* from the Bartonian Gehlbergschichten of Helmstedt is thought to be reworked, see Russell *et al.*, 1982: 13); middle to late Lutetian, ?Auversian, France; late Lutetian to ?Auversian, Switzerland; ?Auversian, Britain.

EMENDED DIAGNOSIS of *L. cuvieri* (translated and slightly modified from Fischer 1964; additions are italicized). Medium-sized species. Maxillary teeth large and rounded (*M^1 length 31 mm*). *Preultimate upper molars slightly broader than long.* Cingula reduced to a minimum. Upper molars with completely tapiroid metacone (the convexity on the outer wall is strong); the parastyle appears rounded and closely fitted to the paracone. *Upper premolars with or without small, poorly differentiated hypocone.* The base of the lingual side of the incisors mostly covered with very strong enamel wrinkles and papillae.

MATERIAL. Left M^3, not *in situ*, but almost certainly from the Elmore Member, Barton Clay Formation, foreshore at Elmore, near Lee-on-Solent, Hampshire. The specimen is in Gosport Museum (GM 978110–3) and a cast (M41977) in the BM(NH). Mr D.J. Kemp of Gosport Museum collected the specimen and presented the cast to the BM(NH).

DESCRIPTION. The tooth is moderately worn so that dentine is continuously exposed from parastyle to protocone and from ectoloph to hypocone. The mesial edge of the tooth is mainly missing as far back as the long axis of the protoloph, except for the buccal region of the parastyle and a small part at the mid-point of the mesial edge below the crown base.

Estimated maximum length perpendicular to the mesial edge is 38·5 mm. Maximum width parallel to the mesial edge is 41·7 mm. Measurements of M^3 from Filhol's (1888*a*) pl. 16, figs 3–4 of the syntype cranium of *L. cuvieri* are 36·4 mm long and 42·0 mm wide, so size and length/width ratio are very similar to this species.

The size, shape and proximity of the parastyle to the paracone is also similar to Filhol's figures of *L. cuvieri*. Only the buccal cingulum is slightly more extensive: it is weakly developed between the parastyle and paracone and is present buccal to the metacone, continuing distally to meet the distal cingulum.

Although M^3 in *Lophiodon* is less distinctive of the 'tapiroid' versus 'rhinocerotoid' condition than are the upper preultimate molars, the Elmore M^3 can be distinguished from that of most other similar-sized species as follows. In *L. isselense* it is relatively longer and narrower and the parastyle is separated from the paracone; in *L. tapiroides*, it is relatively longer and narrower and the parastyle, although no more detached than in *L. cuvieri*, is mesiodistally compressed. In *L. parisiense* it is very similar morphologically, although slightly but significantly smaller. *L. thomasi* from the French Bartonian is probably the species most similar to *L. cuvieri*, being distinguished only by the presence of a distinct P^4 hypocone. The unique holotype consists of an upper incisor, part of P^3?, complete P^4, and M^{1-2} only, so comparison with the Elmore M^3 is not possible. Whereas specific identity with either *L. cuvieri* or *L. thomasi* is equally possible, the determination as *L.* cf. *cuvieri* is considered the more practical alternative.

DISCUSSION. When Depéret (1906) first described *L. thomasi* from the Calcaire de Ducy of Sergy, Aisne, France (see Thomas 1906 for locality details), he distinguished it from *L. parisiense* by its P^4 hypocone, slightly less tapiroid M^{1-2} and slightly larger size. He did not compare it with *L. cuvieri*, from which it differs only in its distinct P^4 hypocone. Fischer (1964: 67, text-fig. 21) considered that *L. thomasi* was derived from *L. parisiense*, but *L. cuvieri* seems a better candidate for ancestry both morphologically and stratigraphically.

Stehlin (1903: 128–146) attributed various cheek teeth from Egerkingen to *L. cuvieri* or '*L. cuvieri*?'. Amongst these he described (1903: 135–136) several P^3s (as 'P^{2}') and P^4s (as 'P^{1}'), mainly from fissure α, as '*L. cuvieri*?' and as having incipient hypocones. They appear thus to form good morphological intermediates between *L. cuvieri* and *L. thomasi*, which, if phylogenetically intermediate, ought to be of Auversian age. Similar incipient hypocone development on P^2s and a P^3 attributed to *L. cuvieri* from the French Auversian locality of Arcis-le-Ponsart (Louis 1976: 50) would seem to confirm both the postulated ancestor–descendant relationship and an Auversian age for Egerkingen α. On the other hand, Sudre (1971: 92) noted beginnings

of hypocone formation on a P^2 and P^3 of *L. cuvieri* from the late Lutetian (similar horizon to the types) of Pargny. So it would appear that large assemblages are necessary to account for individual variation (cf. Sudre, 1971, for *L. lautricense*). Upper premolars are eagerly awaited from the sparsely mammaliferous Elmore site.

Lophiodon cf. *lautricense* Noulet 1851

v. 1977*a* *Lophiodon* cf. *lautricense* Noulet; Hooker: 91–94.
v. *1980* *Lophiodon* cf. *lautricense* Noulet; Hooker & Insole: 43.

Holotype of *L. lautricense*. Mandible with broken teeth. Sables du Castrais; Braconnac, near Lautrec, Tarn, France (Muséum d'Histoire Naturelle de Toulouse, unnumbered).

Range of *L. lautricense*. Marinesian; France, Switzerland, West Germany.

Diagnosis of *L. lautricense*. No formal diagnosis is available, but there are comprehensive accounts by Sudre (1971) and Stehlin (1903).

Material. Right symphysial fragment with roots of P_{2-3} and root and alveolus of P_4 (BGS GSM88617; cast in BM(NH), M31996). For details see Hooker (1977*a*).

Order **ARTIODACTYLA** Owen 1848*b*

Suborder **PALAEODONTA** Matthew 1929*b*

Superfamily **DICHOBUNOIDEA** Gill 1872
(rank emend. Viret 1961)

Family **DICHOBUNIDAE** Gill 1872 (*sensu* Sudre 1978*b*)

Type genus. *Dichobune* Cuvier 1822.

Included genera. *Protodichobune* Lemoine 1891; *Aumelasia* Sudre 1980; *Buxobune* Sudre 1978*b*; *Meniscodon* Rütimeyer 1888; *Mouillacitherium* Filhol 1882; *Hyperdichobune* Stehlin 1910*b*; *Metriotherium* Filhol 1882; *Synaphodus* Pomel 1848; *Messelobunodon* Franzen 1980*a*; ?*Lantianius* Chow 1964; ?*Chorlakkia* Gingerich, Russell, Sigogneau-Russell & Hartenberger 1979.

Range. Late Ypresian–Chattian, Europe; middle to late Eocene, Asia?

Diagnosis. See Sudre (1978*b*: 18).

Genus *HYPERDICHOBUNE* Stehlin 1910*b*

Type species. *Dichobune spinifera* Stehlin 1906. Ludian, Entreroches, Canton Vaud, Switzerland.

Included species. *H. nobilis* (Stehlin 1906) Stehlin 1910*b*; *H. spectabilis* Stehlin 1910*b*; *H. hammeli* Sudre 1978*b*; ?*H. langi* (Rütimeyer 1891) Sudre 1972; *H.* sp. 1 and ?*H.* sp. 2 herein.

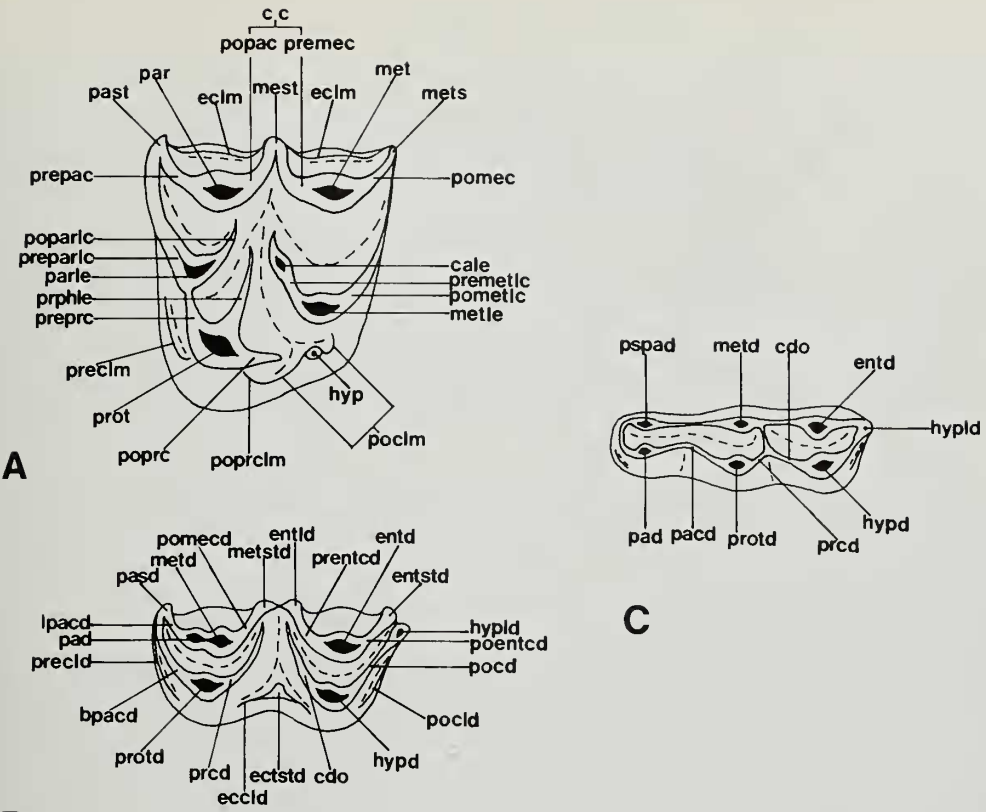
Range. M. Lutetian–Auversian, France; late Lutetian–late Ludian, Switzerland; Marinesian, England.

Diagnosis. See Sudre (1978*b*: 35).

Hyperdichobune sp. 1
(Pl. 28; Table 29)

v. *1977b* ?*Hyperdichobune spectabilis* Stehlin; Hooker: 141.
v. *1980* *Hyperdichobune* sp.; Hooker & Insole: 43.

Material. P^4 (M36800); three $M^{1/2}$s (M36196, M37492, M37710); two M^3s (M37493–4); DP^4 (M37459); $M_{1/2}$ talonid fragment (M37553); M_3 (M36815); lower molar trigonid fragment ? (M36195); and DP_4 talonid fragment (M37496).



Text-figure 54 Dental nomenclature of artiodactyl cheek teeth, modified considerably from Coombs & Coombs (1977: 585, fig. 1). A, left upper molar; buccal edge towards top of page, lingual towards bottom. B, left lower molar, and C, left lower fourth deciduous premolar; buccal edges towards bottom of page, lingual edges towards top.

Abbreviations:

A. cale—central accessory conule
cc—centrocrista
eclm—ectocingulum
hyp—hypocone
mest—mesostyle
met—metacone
metle—metaconule
mets—metastyle
par—paracone
parle—paraconule
past—parastyle
poclm—postcingulum
pomec—postmetacrista
pometlc—postmetaconule crista
popac—postparacrista
poparlc—postparaconule crista
poprc—postprotocrista
poprclm—postprotocingulum
preclm—precingulum
premec—premetacrista
premetlc—premetaconule crista
prepac—preparacrista
preparlc—preparaconule crista
preprc—preprotocrista
prot—protocone
prphle—protolophule

B & C. bpacd—buccal paracristid
cdo—cristid obliqua
eccld—ectocingulid
ectstd—ectostylid
entd—entoconid
entld—entoconulid
entstd—entostylid
hypd—hypoconid
hypld—hypoconulid
lpacd—lingual paracristid
metd—metaconid
metstd—metastylid
pacd—paracristid
pad—paraconid
pasd—parastylid
pocd—postcristid
pocld—postcingulid
poentcd—postentocristid
pomecd—postmetacristid
prcd—protocristid
precld—precingulid
prentcd—pre-entocristid
protd—protoconid
pspad—pseudoparaconid
(of Hershkovitz, 1971).

Table 29 Length (l) and trigonid (w_1) and talonid (w_2) width measurements of teeth of *Hyperdichobune* sp. 1 from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1	w_2
M36800	RP^4	(3·7)	3·5	
M37710	$LM^{1/2}$	(4·1)	–	
M36196	$RM^{1/2}$	(4·5)	4·8	
M37493	LM^3	4·5	(5·0)	
M37494	RM^3	(4·8)	5·4	
M37492	$LM^{1/2}$	(4·5)	4·4	
M37459	RDP^4	(3·8)	(4·0)	
M37553	$RM_{1/2}$	–	–	3·3
M36815	RM_3	–	3·0	2·6
M37496	LDP_4	–	–	2·3

HORIZON AND LOCALITY. Creechbarrow Limestone Formation. Creechbarrow.

DESCRIPTION. P^4: The parastyle, base of paracone and preprotocrista are broken away. There is a large, distally-placed metacone two-thirds the size of the paracone. The distal cingulum is weak and swollen somewhat in the middle. An incomplete buccal cingulum is preserved round the metacone (Pl. 28, fig. 1). *H. spectabilis* from Entreroches (NMB Mt723) has a smaller metacone closer to the paracone; continuous buccal cingulum; stronger, more extensive distal cingulum with larger bulge forming incipient metaconule; and larger protocone with protolophule joining paracone.

$M^{1/2}$: M36196 is heavily worn and very weathered (Pl. 28, fig. 3). It has a large, distally skewed mesostyle; a strong buccal cingulum only between the mesostyle and metastyle; and apparently no lingual cingulum. It evidently had a fairly large hypocone which is completely fused by wear to the metaconule and protocone. The outline is somewhat oblique, the lingual cusps being slightly more mesial than the buccal cusps. Of M37710, only the lingual half remains (Pl. 28, fig. 6). The paraconule is small, close to the protocone, does not bulge mesially and there is a distinct postparaconule crista. The metaconule is nearly as large as the protocone and the hypocone is much smaller. What remains of the outline is similar to M36196. M37492 lacks the metaconal region, is smaller than M36196 or M37710 and may be an M^1 (Pl. 28, fig. 2). It is heavily worn but its development of lingual cusps is very similar to that of M37710. The mesial margin is straight and the parastyle is prominent. *H. spectabilis* M^{1-2} (Mt723) are similar in position of mesostyle, prominence of postparaconule crista and outline; but the hypocone is larger and there is a distinct mesial bulge to the paraconule.

M^3: M37493 (Pl. 28, fig. 7) is a very corroded tooth and thus difficult to compare character for character with M37494 (Pl. 28, fig. 4), whose parastylar area is broken. The latter, however, is slightly larger, seems to have a more rounded outline, stronger cingula and more mesially bulging paraconule. It is thus more like *H. spectabilis* than is M37493, whose paraconule is more like that of the $M^{1/2}$s, M37710 and M37492. Both M^3s have postparaconule cristae and no hypocone, but are relatively shorter teeth than the two known M^3s of *H. spectabilis* (Mt723 and Mt396, the latter figured by Stehlin, 1910*b*: 1100, text-fig. 225).

DP^4: Like M37492, M37459 has lost the metaconal region; it is quite worn, has thinner enamel and is lower-crowned than the molars; and it has a strong parastyle and postparaconule crista (Pl. 28, fig. 5). It appears to have been narrower mesially than distally and there is a strong cingulum round the more buccal protocone. It has more the proportions of the DP^4 of *Mouillacitherium* cf. *elegans* from Mormont (Stehlin 1906: pl. 12, fig. 30) than that of *H. spinifera* (*ibid.*: pl. 12, fig. 40).

$M_{1/2}$: This is very similar to the holotype M_{1-2} of *H. spectabilis*, but the hypoconulid is a larger, distally-projecting cusp and there is no crest joining the cristid obliqua to the entoconid (Pl. 28, fig. 10). The wear state of the two specimens is very similar.

M_3: The hypoconulid lobe is broken away and the tooth is very heavily worn (Pl. 28, fig. 11). The characters that remain visible are similar to *H. spectabilis* but like the $M_{1/2}$ there is no crest joining the cristid obliqua to the entoconid.

$M_{1/2/3}$: This doubtfully attributed trigonid fragment has a distinct paraconid slightly smaller than the metaconid but close to it (Pl. 28, fig. 9). Whether *H. spectabilis* had the same character is difficult to tell as the teeth are much more worn. However, the holotype M_3 has two deep areas of dentine separated by a shallower dentine isthmus; this suggests that intervening enamel had, at only a slightly earlier wear stage, separated a paraconid from a metaconid.

DP_4: This talonid fragment is like the $M_{1/2}$ but smaller, lower-crowned and with thinner enamel, its hypoconulid is more vertically orientated and its outline begins to taper mesially (Pl. 28, fig. 8).

Discussion. Stehlin (1910*b*) could see no difference except size between *H. spinifera* and *H. spectabilis*, both from Entreroches. The only tooth types common to both, however, are P^4–M^1 and P_4–M_1. *H. spinifera* seems nevertheless to have an M^1 with paraconule not mesially salient and weaker cingula; a P^4 with a weaker incipient metaconule and better separated paracone and metacone and no protolophule; and a lower molar without a crest joining the cristid obliqua to the entoconid. From this evaluation and the above description, the Creechbarrow material appears to incorporate characters of both *H. spinifera* and *H. spectabilis*. This could mean that two species each related to those from Entreroches are represented, or that the morphological characters distinguishing the meagre sample of *H. spinifera* and *H. spectabilis* reflect intraspecific variation in a monospecific Creechbarrow assemblage, if not also in the Entreroches assemblages. More specimens are required to test these ideas.

The Creechbarrow teeth do not belong to either *H. hammeli*, *H. nobilis* or ?*H. langi*. The first has a narrower P^4 with small protocone and $M^{1/2}$ apparently with no postparaconule crista. The type series, however, appears to be composite: NMB Bchs430 with its large hypocone and overall arrangements of cusps (Sudre 1978*b*: text-pl. 1, fig. 5) fits the lipotyphlan *Amphilemur leemanni* (whose type locality, Bouxwiller, is the same as that of *H. hammeli*); also the absence of a P_4 hypoconid on the holotype makes it unlikely that the P^4 would have had subequal paracone and metacone like the paratype UM BUX66166 (Sudre 1978*b*: text-pl. 1, fig. 6).

Stehlin (1910*b*: 1101) distinguished *H. nobilis* from *H. spinifera* mainly on the former's less molariform referred P^4 (Stehlin 1906: pl. 12, fig. 25), in which it also differs from *H.* sp. 1.

?*H. langi* is a very different species which may not even belong to this genus (see below under ?*H.* sp. 2).

The $M^{1/2}$ from Lissieu, thought at first by Sudre (1972: 127, text-fig. 5C) to be *H. nobilis* and later (Sudre 1978*b*: 36) to be specifically indeterminate, is similar to the Creechbarrow molars, but from the figure appears to lack a postparaconule crista.

?*Hyperdichobune* sp. 2
(Pl. 29, fig. 6)

v. *1977b* *Rhagatherium* sp.; Hooker: 141.
v. *1980* *Rhagatherium* sp.; Hooker & Insole: 44.

Material. Left $M^{1/2}$ (M37546), right $M^{1/2/3}$ lingual half (M36187); and doubtfully a right $M^{1/2}$ metaconal fragment (M37547).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. M37546 is triangular in outline, slightly broader than long, with the mesiobuccal corner a right angle. Outline and cusp pattern are very similar to *Mixtotherium* but with very small hypocone and a paraconule well separated from the protocone by a fissure. The centrocrista is buccally flexed and there is a large mesostyle. The paracone and metacone are buccally

4
7
11
3
6
10
2
5
9
1b
1a
8

salient and there is no buccal cingulum. The cusps generally appear gracile and are separated by broad deep valleys. The premetaconule crista is short, curving back to join the metacone mesiolingually. The tooth is 5·6 mm long and 6·1 mm wide.

In M36187, the hypocone is little more than a papilla at the distobuccal end of the postcingulum. M37547 shows the metastyle joined to the mesostyle by a buccal cingulum.

Discussion. The affinities are somewhat enigmatic. Strong similarities can be seen with ?*Hyperdichobune langi* from Egerkingen on the one hand and with *Mixtotherium* on the other. Decisions are hampered by only one tooth type being known for ?*Hyperdichobune* sp. 2. It could be doubted that ?*H. langi* is a *Hyperdichobune* for the following reasons. Firstly, on M^2 the near triangular outline tapers distally, the mesiobuccal corner being acute; second, the upper molar paraconule is large and well separated from the protocone; and third, on the upper molars the very weak postparaconule crista is directed towards the mesostyle, not towards the middle of the paracone.

No premolars were recorded for '*Dichobune*' *langi* by Stehlin (1906: 623–625), nor did he (1910*b*) refer it with the other three species to his new genus *Hyperdichobune*. Sudre (1972: 121–126, text-figs 3–4) referred upper and lower molars from Lissieu to the species and included it in *Hyperdichobune* on the basis of an isolated P^3. The P^4 was later considered (Sudre 1978*b*: 36) to be wrongly identified and to require replacing by another one that he had referred to *H. nobilis* (Sudre 1972: 127, text-fig. 5B). The latter tooth is like P^4 of *Mixtotherium* in its more sharply triangular outline, buccal cingulum round the metacone, large, mesially salient parastyle and small paraconule and metaconule. If it really belongs to ?*H. langi*, it suggests a close relationship with *Mixtotherium*; alternatively it may belong to *Mixtotherium infans*.

?*H. langi* M^2 differs from that of ?*H.* sp. 2 from Creechbarrow mainly in being smaller, relatively shorter and having a larger hypocone. *Mixtotherium* differs from ?*H.* sp. 2 in having a strong buccal cingulum, less buccally salient paracone and metacone, the paraconule fused to the protocone and no hypocone. The intermediate state of ?*H.* sp. 2 suggests affinities between ?*H. langi* and *Mixtotherium* and possible derivation of the latter from the Dichobunidae. The absence of either premolars associated with molars or of any known basicranial in ?*H. langi* means that we do not know whether any of the other distinctive features of *Mixtotherium*, such as absence of mastoid exposure, had already evolved in these dichobunids. When better known a new generic name may be found necessary for ?*H. langi* and ?*H.* sp. 2.

Family **MIXTOTHERIDAE** Pearson 1927

Type and only known genus. *Mixtotherium* Filhol 1880*b*. See also comments under ?*Hyperdichobune* sp. 2, above.

Genus ***MIXTOTHERIUM*** Filhol 1880*b*

(Complicated synonymy dealt with by Stehlin, 1908: 799–828).

Type species. *M. cuspidatum* Filhol 1880*b*. Phosphorites du Quercy; France (figured Filhol, 1882: pl. 9, figs 1–7).

Included species. *M. gresslyi* Rütimeyer 1891 (including *M. priscum* Stehlin 1908); *M. infans* Stehlin 1910*b*; *M. leenhardti* Stehlin 1908; *M. depressum* (Filhol 1884) Stehlin 1908; *M. quercyi* (Filhol 1888*b*) Stehlin 1908.

Plate 28 Light macrographs of cheek teeth of *Hyperdichobune* sp. 1 from Creechbarrow, × 9. Occlusal views, except Fig. 1a. Fig. 1a, b, right P^4 (reversed) (M36800). a, buccal and b, occlusal views. Fig. 2, left $M^{1/2}$ (M37492). Fig. 3, right $M^{1/2}$ (reversed) (M36196). Fig. 4, right M^3 (reversed) (M37494). Fig. 5, right DP^4 (reversed) (M37459). Fig. 6, lingual half of left $M^{1/2}$ (M37710). Fig. 7, left M^3 (M37493). Fig. 8, talonid fragment of left DP_4 (M37496). Fig. 9, trigonid fragment of right $M_{1/2/3}$ (reversed) (M36195). Fig. 10, talonid fragment of right $M_{1/2}$ (reversed) (M37553). Fig. 11, right M_3 with broken hypoconulid lobe (reversed) (M36815). See p. 376.

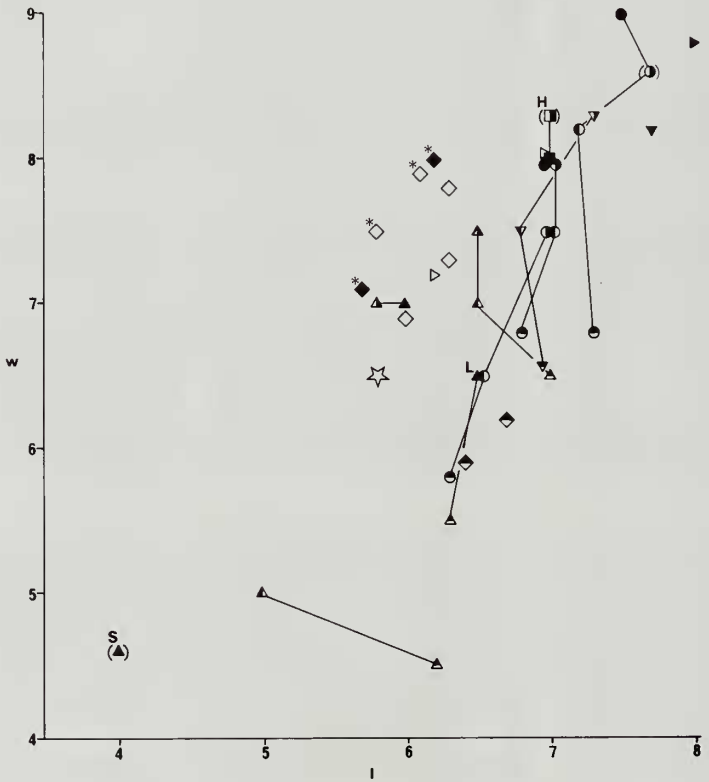
RANGE. Late Lutetian–Ludian; England, France and Switzerland.

DIAGNOSIS. See Viret (1961: 902).

DISCUSSION. This genus is very local in occurrence, being almost entirely restricted to the fissure deposits of Switzerland and France, although it is not uncommon where it occurs. It was recently discovered in the Upper Calcaire Grossier of the Paris Basin (Ginsburg *et al.* 1977) and the Creechbarrow records are the first for England. It has been found in the recent excavations in Le Quercy at the early Ludian sites of La Bouffie and Perrière (Crochet *et al.* 1981).

Once considered related to anoplotheres or anthracotheres, the genus has sometimes been included in the Cebochoeridae (e.g. Sudre 1972; Simpson 1945) because of superficially similar skull shape and lack of mastoid exposure; its possible relationships with the dichobunids are discussed herein under *Hyperdichobune* above.

Of the described species, only *M. cuspidatum*, *M. gresslyi* and *M. infans* are well characterized. *M. quercyi* and *M. depressum* appear very close to typical *M. cuspidatum*, whilst *M. leenhardti* and *M. priscum* are difficult to separate from *M. gresslyi*. *M.* cf. *priscum* and *M.* cf. *gresslyi* from Mormont and Quercy were tentatively separated by Stehlin (1908) from the typical assemblages of these species on stratigraphical, not morphological grounds. It is prob-



Text-figure 55 Scatter diagram of length (l) against width (w) in P^4–M^3 of *Mixtotherium*. □ = *M.* '*priscum*' Stehlin from Egerkingen Huppersand; ▽ = *M.* '*priscum*' from Egerkingen γ; △ = *M. gresslyi* Rütimeyer and *M. infans* Stehlin from Egerkingen α; ◁ = *M.* '*priscum*' from Lissieu; ○ = *M.* 'cf. *priscum*' from the Phosphorites du Quercy; ◇ = *M.* aff. *gresslyi* from Creechbarrow; ☆ = *M.* 'cf. *gresslyi*' from Mormont. * indicates specimens where the parastyle is broken. H = holotype of *M. priscum*; L = lectotype of *M. gresslyi*; S = syntype of *M. infans*. Symbols solid above = P^4; solid on left = M^1; solid on right = M^2; completely solid = M^3; and outline = $M^{1/2}$. Measurements in millimetres. Lines join teeth of one individual.

able that the slightly deeper horizontal mandibular ramus of *M. leenhardti* (Stehlin 1908: text-fig. 129) could result from old age of the individual, as the teeth appear quite worn, compared for instance to his text-fig. 131 of *M.* cf. *priscum*. Gaining an accurate idea of the range of intraspecific variation in this genus is difficult in view of the small number of specimens and the poor locality and stratigraphical data for the old Quercy material. The larger collections from Egerkingen, including those from Egerkingen γ made after Stehlin's publication of *Mixtotherium*, offer better potential. The Creechbarrow material, although not including osteological parts, consists of enough teeth to demonstrate variation for a number of features. A revision of the complete genus is highly desirable.

From the scatter diagram (Text-fig. 55), the Creechbarrow material makes a plot intermediate between *M. gresslyi* and *M. priscum* according to Stehlin's concepts. However, Stehlin (1908: 822) also thought that *M. priscum* might in the light of further material be divided into two or three species. He was struck by its high morphological variation. He could not convincingly separate it morphologically from *M. gresslyi* except by referring the very small individual from Egerkingen α (NMB Eg159; Stehlin 1910*b*: pl. 17, fig. 21), with more quadrate M^1 and elongated P^4, to the latter species. In Text-fig. 55, Eg159 plots closer to the figured syntype M^3 of *M. infans* than to the type M^1 of *M. gresslyi*. Sudre (1972: 133–134, fig. 9) described and figured *M. gresslyi* from Lissieu, but in size his material (isolated upper molars) is close to Eg159 and *M. infans*. His figures suggest that in morphology it differs too; its high selenodonty, deeply incised parastyles and in one case (1972: fig. 9c) absence of paraconule more closely resemble the xiphodont *Haplomeryx*. Text-fig. 55 shows no clear size difference between *M. gresslyi* and *M. priscum* if one excludes Eg159. *M. priscum* from Egerkingen α can easily be accommodated within *M. gresslyi*, whose type is from the same fissure. The assemblages of *M. priscum* from Egerkingen Huppersand (grey marl facies) and Egerkingen γ appear slightly larger, but more specimens would almost certainly produce a normal range overlapping extensively with *M. gresslyi*. The differences are no greater than would be expected from assemblages of one species from different localities or slightly different stratigraphical horizons. It is proposed here that the species *M. priscum* be synonymized with *M. gresslyi*, whilst recognizing that a subspecific difference might be demonstrated if a systematic study of the Egerkingen material were undertaken. Table 30 compares coefficients of variation of various combinations of the different assemblages. The Creechbarrow assemblage (here referred to as *M.* aff. *gresslyi*) is intermediate in size between the Egerkingen γ/Huppersand assemblages ('*M. priscum*') and the Egerkingen α assemblage (type *M. gresslyi*). It is possibly closer to the latter.

Mixtotherium aff. *gresslyi* Rütimeyer 1891
(Pl. 29, figs 1–4; Pl. 30; Text-fig. 55; Tables 30–33)

v. *1977b* *Mixtotherium priscum* Stehlin; Hooker: 141.
v. *1980* *Mixtotherium priscum* Stehlin; Hooker & Insole: 44.

LECTOTYPE of *M. gresslyi* (following Sudre 1972: 133, as 'type'). Right maxillary fragment with P^2–M^1. Auversian, Egerkingen α; Canton Solothurn, Switzerland (figured Rütimeyer 1891: pl. 6, fig. 1 and Stehlin 1908: 817, text-fig. 129).

Table 30 Coefficients of variation (v) for length of $M^{1/2}$ in *Mixtotherium* assemblages. N = number of specimens.

Assemblages	N	v
M. gresslyi and *M.* '*priscum*' from Egerkingen α	4	5·53
Ditto and *M.* 'cf. *gresslyi*' from Mormont	5	6·16
Ditto and *M.* aff. *gresslyi* from Creechbarrow	11	4·68
Ditto and *M.* '*priscum*' from Egerkingen γ and Huppersand	14	7·34
M. '*priscum*' from Egerkingen γ and Huppersand and *M.* aff. *gresslyi* from Creechbarrow	9	8·04
M. aff. *gresslyi* from Creechbarrow	6	3·19

MATERIAL. Two P^3s, broken mesially (M37505, M37559); two P^4s (M37506–7); five $M^{1/2}$s, one fragmentary (M36184, M37509–10, M37514, M37512); seven M^3s, three fragmentary (M36185–6, M37508, M37515, M37511, M37513, M37516); three fragmentary upper molars (M36818, M37517–8); two $P_{2/3}$ talonid fragments (M36438, M37560); two P_3s lacking mesial half (M36797, M37558); two P_4s lacking talonids (M37519–20); seven $M_{1/2}$ talonid fragments (M36193, M36796, M36809–10, M37522–4); two M_3 talonid fragments (M36408, M36500); nine lower molar trigonid fragments (M36188–9, M36198, M36827, M37521, M37525–7, M37711); two DP_2? fragments (M36416, M36808); DP_3? talonid fragment (M36194); two DP_4 trigonid fragments (M36411, M37550).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

RANGE OF THE SPECIES (including aff. and cf.). Late Lutetian, France and Switzerland; Auversian, Switzerland; Marinesian, England and Switzerland; and ?Marinesian and Ludian, France.

EMENDED DIAGNOSIS OF SPECIES. Medium-sized species (mean length of $M^1 = 6{\cdot}5$ mm); upper molars broader than long (length *c.* 80% of width); depth of adult mandibular ramus beneath the distal end of M_3 2·5 times length of M_3.

DIFFERENTIAL DIAGNOSIS. *M. cuspidatum* is larger; has upper molars with approximately equal length and width; and deeper mandible. *M. infans* is smaller.

Table 31 Length (l) and width (w) measurements of upper teeth of *Mixtotherium* aff. *gresslyi* from Creechbarrow. Measurements in millimetres. *indicates parastyle missing.

No.	Tooth	l	w
M37505	RP^3	–	3·9
M37559	RP^3	–	4·0
M37506	LP^4	6·7	6·2
M37507	RP^4	6·4	5·9
M36184	$LM^{1/2}$	6·0	6·9
M37509	$LM^{1/2}$*	6·1	7·9
M37510	$LM^{1/2}$*	5·8	7·5
M37514	$RM^{1/2}$	6·0	–
M36185	LM^3	6·3	7·3
M37508	LM^3*	5·7	7·1
M37515	LM^3*	6·2	8·0
M36186	RM^3	6·3	7·8

Table 32 Trigonid (w_1) and talonid (w_2) width measurements of lower teeth of *Mixtotherium* aff. *gresslyi* from Creechbarrow. It was not possible to measure length in any of these teeth. Measurements in millimetres.

No.	Tooth	w_1	w_2
M36438	$LP_{2/3}$	–	3·0
M36797	LP_3	–	3·5
M37558	LP_3	–	3·5
M37560	RP_3	–	2·7
M37519	LP_4	3·4	–
M37520	RP_4	3·4	–
M36796	$LM_{1/2}$	–	4·5
M37522	$LM_{1/2}$	–	4·2
M36193	$RM_{1/2}$	–	4·1
M36809	$RM_{1/2}$	–	3·6
M37523	$RM_{1/2}$	–	3·8
M37524	$RM_{1/2}$	–	4·7
M36500	LM_3	–	4·5
M36189	$LM_{1/2/3}$	4·0	–
M37521	$LM_{1/2/3}$	4·2	–
M37525	$LM_{1/2/3}$	4·0	–
M37526	$LM_{1/2/3}$	4·5	–
M36188	$RM_{1/2/3}$	4·1	–
M37527	$RM_{1/2/3}$	4·2	–
M37711	$RM_{1/2/3}$	3·9	–
M36808	LDP_2?	2·0	–
M36416	RDP_2?	1·9	–
M36194	LDP_3?	–	2·7
M37550	RDP_4	3·0	–

DESCRIPTION. Comparison is made with a maxilla from the Quercy Phosphorites (M33522), casts of a maxilla (NMB Eh409) and mandibular ramus (Eh424) from Egerkingen γ and original M^3 (M12017), mandibular ramus (M12015) and M_3 (M12016) from Egerkingen undifferentiated (although the ochreous sandy bolus matrix suggests fissure γ also); as well as with Stehlin's figures (1908, 1910*b*).

P^3: Both teeth are broken mesially through the paracone. Their metacone is larger and better separated from the paracone than on Eh409 and M33522. In fact the metacone is nearly as large as the paracone. The protocone is also larger in M37559 than on these two and M37505.

P^4: Both have strongly buccally flexed centrocristae and strong mesostyles – more so than M33522. There is a strong buccal cingulum on M37506 behind the mesostyle, which broadens the stylar shelf and pushes the metacone further from the buccal margin than is the case in M37507. In the latter the buccal cingulum is restricted to the mesial side of the metastyle. The metaconule is larger in M37507 and has a premetaconule crista joining it to the metacone at a mesiolingual position. The parastyle is more mesially salient in M37506 than M37507. Both have overall smaller parastyles than M33522.

Upper molars: See Table 33 for the distribution of the main variable characters. There is a partial positive correlation between length of the premetaconule crista and the proximity of the paraconule to the protocone; otherwise the characters appear randomly distributed. There is nothing to suggest that more than one species is represented. M^3 can generally be distinguished from M^1 or M^2 (when absence of a recognizable distal interstitial facet is unreliable), by being relatively longer and having a more lingually displaced metacone.

P_{2-3}: Two specimens from Egerkingen γ show P_3 to be very variable in this assemblage. One (M12015) resembles the P_2 of another (Eh424) in the small size of the hypoconid, absence of a metaconid and shallow lingual concavity of the protoconid–paraconid–parastylid crest. The P_3 of Eh424, on the other hand, has a small distolingual metaconid joined to the protoconid by an oblique protocristid; the larger hypoconid is slightly displaced buccally; and the protoconid–paraconid–parastylid crest is more deeply concave lingually. On this basis, the distal fragment (M36438) from Creechbarrow could be either a P_2 or a simple P_3. Size favours it being a P_2. On this basis, it could also be argued that the equal-sized M37560 (also a distal fragment), with a small metaconid close mesiolingually to the hypoconid, might be a complex P_2 rather than a P_3. M36797 and M37558 are convincing P_3s. They are better preserved but still incomplete mesially. Both have equal-sized metaconids which lie equidistantly distolingual to the protoconid and mesiolingual to the hypoconid, but, unlike Eh424, displaced from the lingual tooth edge and with distolingual oblique crests. The hypoconid on M37558 is smaller than on M36797 and the same size as the metaconid. The cristid obliqua lives up to its name on M36797 (as on Eh424) but is near longitudinal on M37558.

P_4: Both are trigonid fragments which show a buccal paraconid opposite a large lingual pseudoparaconid and a buccally concave paracristid. The specializations here are thus reminiscent of those of an artiodactyl DP_4. That these are not DP_4s is corroborated by enamel thickness and the presence at Creechbarrow of two DP_4s referable to this species. One of the latter is complete enough to show a better divided mesial lobe with the pseudoparaconid larger than the paraconid. Stehlin (1908: 826–7; 1910*b*: pl. 20, figs 4, 12–13, 47) had some problems distinguishing between the two tooth types. Identification of Ef209 as a DP_4 was based on narrower outline and pseudoparaconid higher than paraconid. Whether the morphology of the Creechbarrow P_4s occurs in *M. gresslyi* from Egerkingen depends on whether Stehlin's (1910*b*: pl. 20, fig. 47) enigmatic tooth (NMB Ef238) is a P_4 or DP_4. However, Ef238 has a pseudoparaconid larger than the paraconid, not the other way round, and it could be argued that the Creechbarrow specimens are constant for this character. There is a slight difference in size of the parastylid between the two Creechbarrow P_4s, but otherwise they are remarkably similar.

Lower molars: These are all fragmentary, mainly having been broken into trigonid and talonid parts. The parastylid varies somewhat in strength (Pl. 30, figs 7–8); in two specimens it

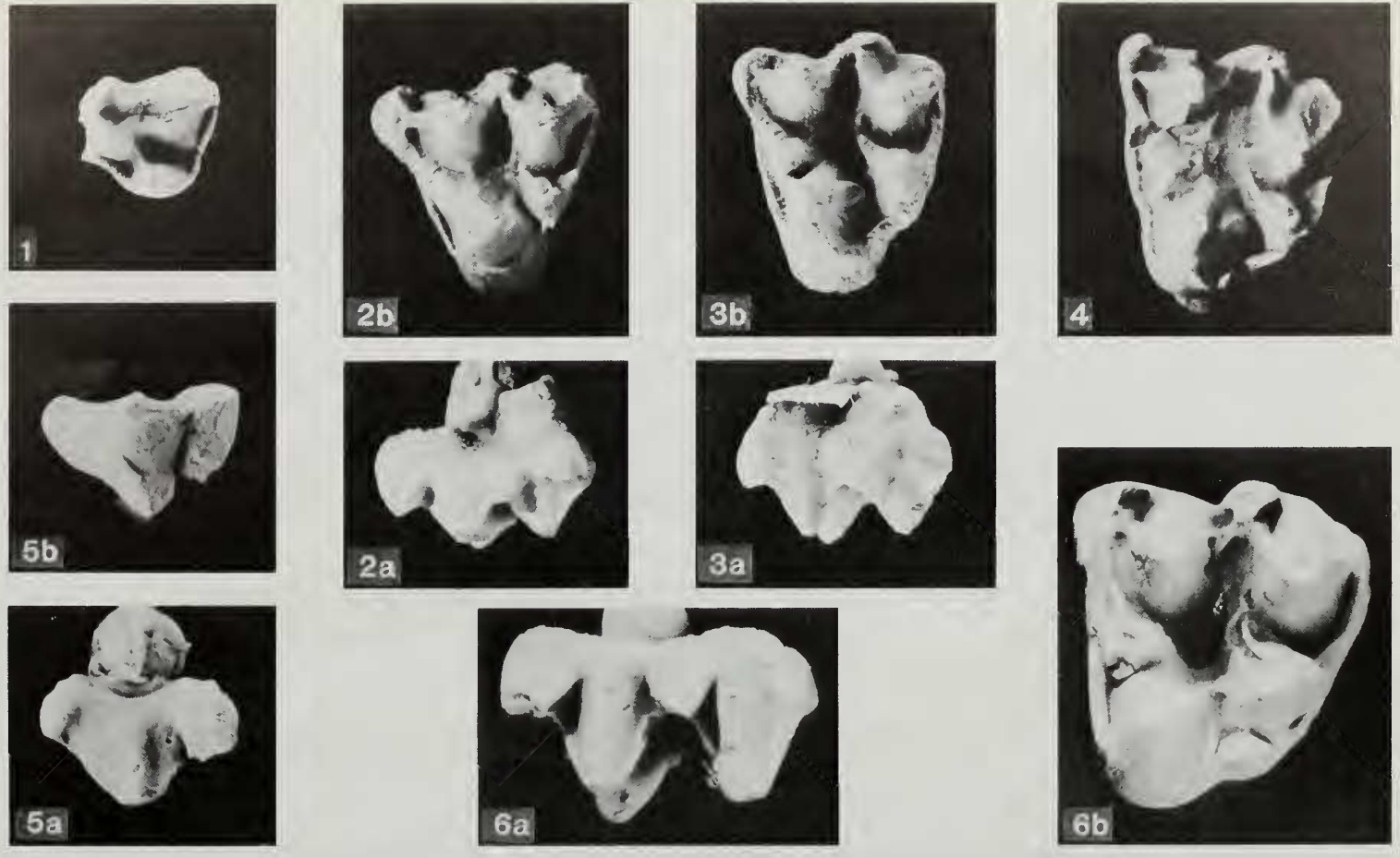


Plate 29 Light macrographs of upper cheek teeth of *Mixtotherium* aff. *gresslyi* Rütimeyer, ?*Mixtotherium* sp. indet. and ?*Hyperdichobune* sp. 2, from Creechbarrow. Views are buccal (a) and occlusal (b or unsuffixed).

Figs 1–4 *Mixtotherium* aff. *gresslyi* Rütimeyer, × 5·5. Fig. 1, right P^3 (reversed) (M37505). Fig. 2a, b, left P^4 (M37506). Fig. 3a, b, left $M^{1/2}$ (M36184). Fig. 4, left M^3 (M36185). See p. 383.

Fig. 5a, b ?*Mixtotherium* sp. indet. Left DP^3? (M36813), × 9. See p. 389.

Fig. 6a, b ?*Hyperdichobune* sp. 2. Left $M^{1/2}$ (M37546), × 8. See p. 379.

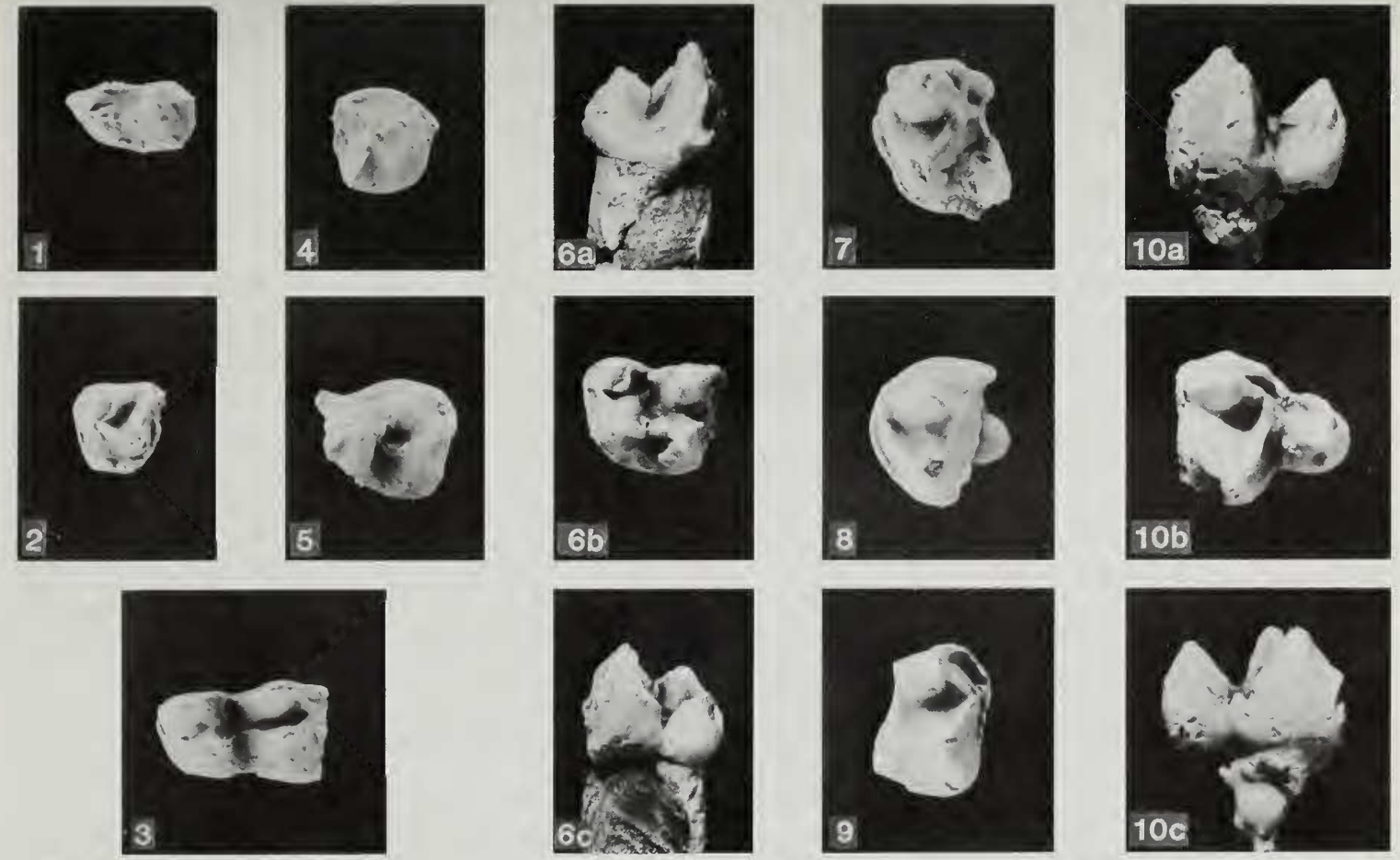


Plate 30 Light macrographs of lower cheek teeth of *Mixtotherium* aff. *gresslyi* Rütimeyer from Creechbarrow, × 5·5. Views are buccal (a), occlusal (b or unsuffixed) and lingual (c). Fig. 1, left DP_2 (M36808). Fig. 2, left DP_3 (M36194). Fig. 3, right DP_4 trigonid fragment (reversed) (M37550). Fig. 4, left P_2? talonid fragment (M36438). Fig. 5, left P_3 broken mesially (M37558). Fig. 6a–c, left P_4 (M37519). Fig. 7, left $M_{1/2/3}$ trigonid fragment (M37525). Fig. 8, left $M_{1/2/3}$ trigonid fragment (M37526). Fig. 9, left $M_{1/2}$ talonid fragment (M37522). Fig. 10a–c, left M_3 talonid fragment (M36500). See p. 383.

Table 33 Distribution of intraspecifically variable characters in upper molars of *Mixtotherium* aff. *gresslyi* from Creechbarrow.

No.	Tooth	mesostyle loop	extent of premetaconule crista as fraction of distance from metaconule to mesostyle	distance of paraconule from protocone as fraction of distance from protocone to paraconule	extent of lingual cingulum	extent of post-cingulum	extent of buccal cingulum
M36184	$M^{1/2}$	open	$>\frac{1}{2}$	$\frac{2}{5}$	postproto-cingulum	just to metaconule	absent parastyle–mesostyle
M36190	$M^{1/2}$	open	–	–	–	–	–
M37509	$M^{1/2}$	widely open	$\frac{1}{3}$	$\frac{1}{3}$?	postproto-cingulum	$\frac{1}{2}$ round metaconule	–
M37510	$M^{1/2}$	narrowly open	$\frac{1}{2}$	$\frac{2}{5}$	postproto-cingulum	just to metaconule	continuous
M37512	$M^{1/2}$	–	–	$\frac{1}{3}$?	round protocone	all round metaconule	–
M37514	$M^{1/2}$	closed	*c.* $\frac{1}{2}$	–	–	–	between parastyle and adjacent stylar cuspule
M36185	M^3	widely open	$\frac{1}{2}$	$\frac{2}{5}$	postproto-cingulum	$\frac{1}{2}$ round metaconule	absent parastyle–mesostyle
M36186	M^3	widely open	$<\frac{1}{2}$	$\frac{1}{3}$	round protocone	$\frac{1}{2}$ round metaconule	?absent parastyle–mesostyle
M37508	M^3	closed	$\frac{1}{3}$	$\frac{1}{3}$	–	–	continuous
M37511	M^3	open?	$>\frac{1}{2}$	–	–	just to metaconule	–
M37513	M^3?	open	$<\frac{1}{2}$	–	–	–	broken in front of mesostyle
M37515	M^3	widely open	$\frac{1}{3}$	$\frac{1}{3}$	postproto-cingulum	–	broken at least behind mesostyle
M37517	$M^{1/2/3}$	–	$\frac{1}{3}$?	–	postproto-cingulum	$\frac{1}{2}$ round metaconule	–
M37518	$M^{1/2/3}$	–	–	–	postproto-cingulum	just to metaconule	–

is nearly as weak as in the *M. gresslyi* specimens from Egerkingen *γ*. A typical character of *Mixtotherium* M_{1-2}s is the presence of a distal cingulum which loops round the distolingual corner of the tooth from the hypoconid to run up the distal wall of the entoconid. On some Creechbarrow specimens it is joined to the postcristid by a median to near lingual crestiform hypoconulid; on all the specimens the lingual limb of the postcristid is present although it may not reach the tip of the entoconid (sometimes missing on *M. cuspidatum*); on one specimen the distal cingulum does not extend buccally from the hypoconulid.

DP_2?: Only mesial fragments are preserved. They are similar to Stehlin's figured DP_4 from Mormont (see p. 385) but are narrower and the metaconid appears to have been absent. M36808 has a parastylid which is slightly smaller than the paraconid and is situated mesio-

lingually to it. An extra small stylar cusp occurs mesial to the parastylid and makes the mesial outline taper to a point. The buccal cingulum is papillate and the lingual cingulum is weak and interrupted. M36416 is broken mesially as well as distally but seems to be beginning to broaden just before the mesial truncation. A very small cusp at the level of the non-existent lingual cingulum and distolingual to the large protoconid may represent the metaconid. A steep longitudinal protocristid bypasses it and is truncated by the distal breakage (cf. Stehlin 1910*b*: pl. 20, fig. 24).

DP_3: M36194 is lower-crowned and has thinner enamel than the P_3s. It has a similar arrangement of cusps but the postcristid reaches the lingual margin at a small entoconid with a sharp distal crest; the cristid obliqua is only slightly oblique; and what is preserved of the confluent distal and buccal cingula is strong and papillate. Compared with the DP_3 that Stehlin figured from Mormont (1910*b*: 1116, text-fig. 231) the metaconid appears to extend further lingually and the cingula appear stronger, but the figure is not clear on the latter point.

DP_4: M37550 is a trigonid fragment which differs from Stehlin's (1910*b*: pl. 20, fig. 12) figure in its more transverse relationship between the protoconid and metaconid and is slightly narrower in outline. M36411 is more fragmentary but shows the protoconid and metaconid to have a more oblique relationship than Stehlin's specimen. Variation appears to be high in this tooth.

Discussion. It is difficult to judge the significance of the more obvious differences between the Creechbarrow assemblage and the various Egerkingen assemblages. The relative constancy of the position of the P_3 metaconid, the large P^3 metacone and the P_4 paraconid lobe, the last two perhaps being linked by occlusal relationships, suggest specializations in the Creechbarrow assemblage. Some evidence for variation in these characters in *M. gresslyi* and *M. cuspidatum*, however, demands a cautious approach. A statistical study of the genus could be enlightening.

?***Mixtotherium*** sp. indet.
(Pl. 29, fig. 5)

Material. Left DP^3? (M36813).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description and discussion. Length is 3·6 mm. The outline is wedge-shaped, the enamel thin, and the tooth is fairly worn and broken distolingually where a protocone was probably once present. The paracone is by far the largest cusp. The parastyle is large and buccally as well as mesially salient. The metacone is very small and only lingually salient, a feature increased by wear from the hypoconid of a $?DP_3$. The distal third of the buccal edge bulges and is bent buccally. A weak mesiolingual cingulum is raised high on the flank of the paracone.

This tooth differs from the DP^3 of *Mixtotherium cuspidatum* figured by Stehlin (1908: 803, text-fig. 120) in being much smaller and less molariform. The latter has a mesostyle, a large metacone and a crest joining the metacone to the protocone. Evidence for possible attribution of the Creechbarrow specimen to *Mixtotherium* comes from a referred DP^3 of *M.* '*priscum*' (= *M. gresslyi*, see p. 383) from Egerkingen γ (NMB Eh414). This tooth is associated in a maxillary fragment with a DP^4 which is likewise far less molariform than that of *M. cuspidatum*. The Egerkingen γ DP^3 is very similar to M36813. It differs in being nearly twice the linear size; in having a straighter buccal edge with a buccal cingulum bordering the metacone; and in having a lower mesiolingual cingulum.

The size of M36813 would be appropriate to that of *M. infans* but no DP^3s have been attributed to this species. Specific identification based on this single tooth would be unreliable.

Family **CEBOCHOERIDAE** Lydekker 1883

Type genus. *Cebochoerus* Gervais 1852.

Included genera. *Acotherulum* Gervais 1850 (?including *Moiachoerus* Golpe-Posse 1972, *fide* Sudre 1978*b*: 82) and Gen. nov. (for *Choeromorus* Gervais 1852, *sensu* Jaeger 1971).

RANGE. Middle Lutetian to early Stampian, Europe.

DIAGNOSIS. See Sudre (1978*b*: 49).

INTRODUCTION. This small family has long been the subject of discussion over generic content and nomenclatural priorities (e.g. Stehlin 1908, Depéret 1917, Pearson 1927, Sudre 1978*b*). The main causes of these problems are the rather low anatomical diversity (taxonomic differences often being minor and easily confused with intraspecific variation) and the poor quality or loss of type specimens. A preoccupation with increase in size as the main criterion in the recognition of lineages has also impeded the unravelling of the morphological details of the group.

The problem of the genus *Choeromorus* (*sensu* Stehlin 1908), whose only difference from *Cebochoerus* was supposed to be the presence of enlarged pig-like lower canines and extrapolated small first premolars, was essentially overcome by Sudre (1978*b*: 52–54); he considered the affinity of the canines, which were isolated, with the Cebochoeridae to be unproven and that the problem therefore never really existed. The probability that these teeth belong to palaeotheres is discussed herein above under *Lophiotherium* (p. 352).

The problem caused by synonymy of the type species of *Cebochoerus* and *Acotherulum* was discussed by Sudre (1978*b*: 49–51). He proposed the changing of the type species of *Cebochoerus* to *C. lacustris* (following the apparent sentiments of Gervais (1859: 198)) in order to stabilize the Cebochoeridae type genus and to maintain its 'common usage' distinction from *Acotherulum*. No formal proposal has yet been made to the ICZN regarding this change of type species. Sudre's separation of the two genera is followed here, but a different content of species for each is shown to be necessary. It is worthy of note that the holotype of *C. anceps* is no longer missing (as recorded by Depéret 1917: 102 and Sudre 1978*b*: 50) but is in the collections of the University of Lyon (FSL 6796).

Genus ***CEBOCHOERUS*** Gervais 1852 (*sensu* Gervais 1859)

[incl. *Cebochoerus* (*Gervachoerus*) Sudre 1978*b* in part]

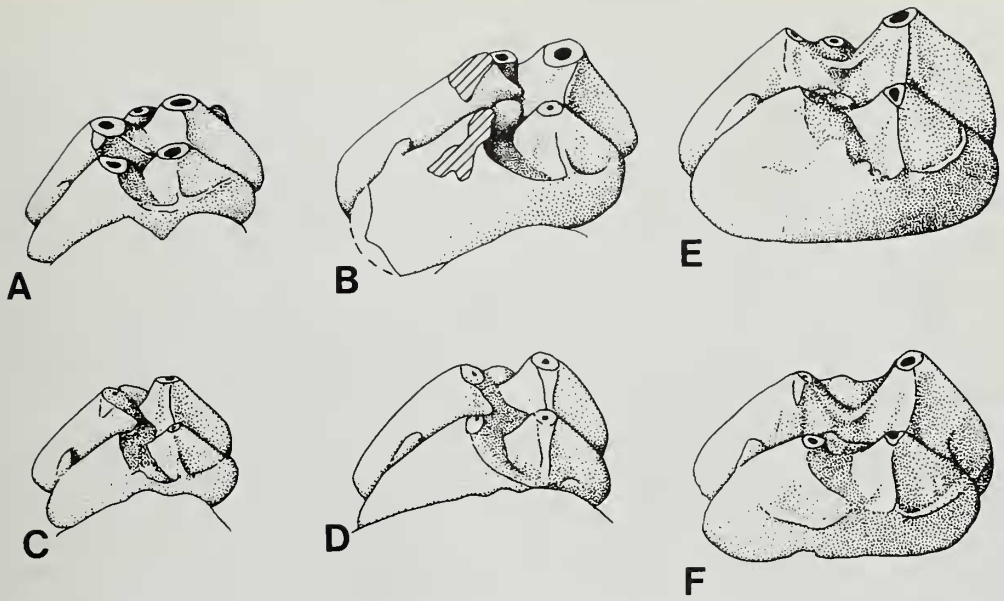
TYPE SPECIES. *C. anceps* Gervais 1852. Ludian; La Débruge, Vaucluse, France. This is pending formal application to the ICZN for change of type species to *C. lacustris* Gervais 1856 (from the Ludian limestone of Souvignargues, Gard, France), the holotype of which was reported lost by Sudre (1978*b*: 74).

INCLUDED SPECIES. *C. lacustris* Gervais 1856; *C. minor* Gervais 1876 (including *C. helveticus* (Pictet & Humbert 1869) Sudre 1978*b*); *C. ruetimeyeri* Stehlin 1908; *C. robiacensis* Depéret 1917; *C. fontensis* Sudre 1978*b*; and *C.* aff. *fontensis*.

RANGE. Late Lutetian–late Ludian; England, France, Switzerland and Spain.

EMENDED DIAGNOSIS. $P\frac{1}{1}$ large and caniniform; C_1 incisiform. Upper cheek teeth with strong mesial and distal cingula and crests. Upper molars with: large paraconule; lingual crown height $\geqslant$ buccal crown height; fused lingual roots; postprotocrista restricted to distal wall of protocone; protolophule which may or may not join paracone. P^4 protocone lingual to paracone. P^3 protocone lingual or distolingual to paracone; P^3 outline may or may not narrow mesially. P^2 protocone present or absent. Lower molars with angles of protoconid and hypoconid crests acute. Supraorbital foramina above level of M^2 or M^3. Adult horizontal mandibular ramus about twice as deep below M_3 as below P_2.

SIGNIFICANCE OF THE SUBGENUS *Gervachoerus*. Sudre (1978*b*: 56–57) erected his new subgenus with *C. minor* as its type species. The characters which he used, however, were based on a referred cranium and mandible from Euzet (figured by Depéret 1917: pl. 17, figs 4–6). Contrary to his diagnosis of *Gervachoerus*, the holotype maxilla of *C. minor* (MNHN Qu60b) has upper molars with central accessory conules, and a topotype maxilla (MNHN Qu71) has P^3 roots indicating a longer, narrower tooth than P^4 and which is broader distally than mesially. Material from Lamandine (the type locality) is not complete enough to comment on the other characters listed for *Gervachoerus*, but the only species known to have the mandible shallow



Text-figure 56 Disto-occlusal views of upper preultimate molars of *Cebochoerus* and *Acotherulum*, about ×4. A, left M^2 of *C. fontensis* Sudre (UM F4-214) from Fons 4; B, left M^2 of *C.* aff. *fontensis* (UL 6145) from Euzet; C, right M^2 (reversed) of *C. robiacensis* Depéret (M7528) from Caylux; D, right M^1 (reversed) of *A. quercyi* (Stehlin) (MNHN Qu7075) from Bach; E, left M^1 of *C. 'helveticus'* (Pictet & Humbert) (LGM LM808) from Mormont; F, left M^1 of *C. minor* Gervais (MNHN Qu11283) from Lamandine. A, B, D, E and F are drawn from casts.

from front to back is '*G.*' *campichii*, here shown to belong to *Acotherulum* (see p. 399). The presence on the upper molars from Lamandine of a protolophule joining the paracone and almost equal buccal and lingual crown height indicates close relationships with *C. lacustris* and *C. helveticus* (which Sudre referred to the nominate subgenus) rather than to the Euzet skull or to other species Sudre placed in *Gervachoerus*, such as *G. fontensis* (see Text-fig. 56).

It is concluded that: 1, *Gervachoerus*, based as it must be on *C. minor*, is not sufficiently distinct from the nominate subgenus, based on *C. lacustris*, to warrant subgeneric separation; 2, Sudre's concept of *Gervachoerus* is almost entirely a phylogenetic one which includes species attributable on characters to both *Cebochoerus* and *Acotherulum*; and 3, the Euzet material cannot belong to *C. minor* and requires a new specific name, if it is not conspecific with *C. fontensis* (it is referred to here as *C.* aff. *fontensis*).

Cebochoerus minor Gervais 1876
(Pl. 31, fig. 1; Text-figs 57, 58B, 59, 60A)

v. *1972* *Cebochoerus* sp.; Hooker: 180–181.
v? *1977b* Creodonta or Carnivora indet.; Hooker: 141.
v. 1978*b* *Cebochoerus helveticus* (Pictet & Humbert)?; Sudre: 72, 74.
v. *1980* *Cebochoerus* sp. 1; Hooker & Insole: 44.

HOLOTYPE. Left maxilla with M^{1-3} (MNHN Qu60b). Early Ludian limestone; Lamandine, Quercy, France (see Pl. 31, fig. 2). This specimen was to have been figured by Gervais (1876: pl. XI, figs 7–8), but his plate XI appears never to have been published.

RANGE OF SPECIES. Marinesian, England; early Ludian, France and Spain; probably Marinesian, Switzerland and France.

MATERIAL. Slightly crushed cranium in three pieces, lacking braincase, and with crowns of left P^3–M^3 and right P^4–M^1; roots of left and right C^1–P^1 and left P^2; and alveoli of right I^{2-3} (M26649).

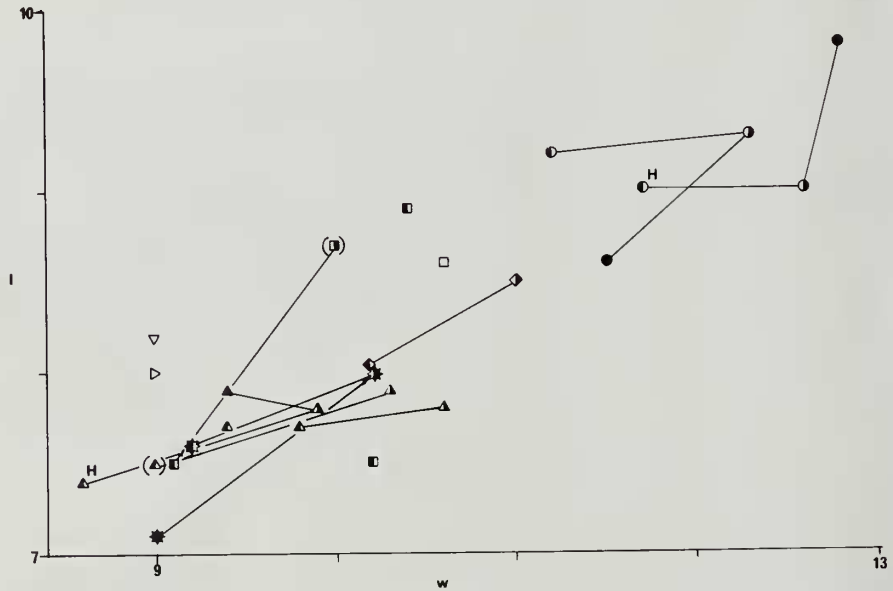
HORIZON AND LOCALITY. Bed C (0·6 m (= 2 ft) below top nodule band), Barton Clay Formation, Barton Cliff, east of Chewton Bunny, Hampshire. In wavewashed lower part of cliff at about SZ 226930. Collected by Mr & Mrs P. Clasby.

DOUBTFULLY REFERRED MATERIAL. Five mainly poorly-preserved anterior permanent and/or deciduous lower premolars (M36199, M36403, M36801, M37551, M37565) from the Creechbarrow Limestone Formation, Creechbarrow.

EMENDED DIAGNOSIS. Medium-sized *Cebochoerus* (mean length of M^1 = 7·5 mm; see Text-fig. 57). Upper molars with: protolophule joining paracone; and lingual crown height = buccal crown height. P^4 width/length ratio 1·4. P^3 with protocone distolingual to paracone; and outline narrowing mesially. [Crown of P^2 unknown]. Supraorbital foramina above level of M^3. Frontals not extended posteriorly from postorbital processes.

DESCRIPTION OF CRANIUM. The specimen is very fragile and after being cleaned of matrix was filled with carbowax to give it support. Slight crushing has bent the ventral part of the left maxilla, posterior to the infraorbital foramen, plus the jugal, the ventral half of the lacrymal and the palate in a medial direction, so that in ventral view the teeth anterior to left P^3 appear to splay laterally. The left nasal and frontal have detached from the maxilla at the intervening sutures and slid beneath it slightly. The result in dorsal view is that the midline suture has come to lie nearer to the left than the right maxilla.

Incisors. The right premaxilla has a complete circular alveolus for I^3. It is about 20° from the vertical and not separated from the canine by a diastema. Parts of the I^2 alveolus are present,



Text-figure 57 Scatter diagram of length (l) against width (w) in upper molars of the *Cebochoerus minor/helveticus/lacustris* complex. ○ = *C. lacustris* Gervais from Souvignargues (H = holotype) and Mémerlein; □ = *C. 'helveticus'* (Pictet & Humbert) from Mormont; △ = *C. minor* Gervais from Lamandine; ▽ = *C. minor* from Sosis; ▷ = *C. minor* from Le Bretou; ◇ = *C. minor* from Fons 6; ☆ = *C. minor* from Barton. Symbols solid on left = M^1, solid on right = M^2; completely solid = M^3; outline = $M^{1/2}$. Measurements in millimetres. Lines join teeth of one individual.

anteromedial to 1^3 and orientated at about 45° to the vertical. There is no evidence for an 1^1 but there would be room for it between I^2 and the midline. In the Mémerlein cranium of *C. lacustris*, the premaxilla appears blunter anteriorly than that of M26649 with the incisor alveoli more transversely orientated. There may, however, be some distortion in the Mémerlein specimen, hidden beneath a crust of matrix. No other known cebochoerid crania have this region preserved.

Canines. These are two-rooted and only slightly smaller than the right canine of *C. lacustris* (proportional with the cheek teeth). The upper canine of the Euzet *C.* aff. *fontensis* cranium appears both proportionally and absolutely smaller.

Premolars. Like the canines, the P^1s are two-rooted and absolutely but not proportionally slightly smaller than those of *C. lacustris*, but are both absolutely and proportionally larger than those of *C.* aff. *fontensis*. They are separated from both canines and P^2s by short diastemata as in these other two species.

The two roots of P^2 have been damaged by the axis of diagenetic bending of the cranium.

P^3 is long, narrow and wedge-shaped with a small distolingual protocone, which makes the tooth wider distally then mesially. The roots on a topotype of *C. minor* (MNHN Qu71; Pl. 31, fig. 3) suggest a similar crown morphology. Both are certainly very different from *C.* aff. *fontensis* whose P^3 has a large lingual protocone. *C. lacustris* from Mémerlein and *C.* '*helveticus*' (Stehlin 1908: pl. 14, fig. 17) have a P^3 protocone larger than that of the Barton specimen, but like the latter and unlike *C.* aff. *fontensis* it is distolingual in position. In the Barton specimen there is a small metacone midway along the postparacrista, as in *C. lacustris* and *C.* '*helveticus*' and unlike *C.* aff. *fontensis*.

The P^4s are transverse and triangular, with pre- and post-cingula which do not meet round the protocone. There is a distal accessory conule, more distinct on the right than on the left tooth. *C.* '*helveticus*' (NMB Mt2) has a very similar P^4. On the Mémerlein *C. lacustris*, the pre- and post-cingula are stronger, the former bypassing the postprotocrista and fusing with the 'paracingulum'. *C.* aff. *fontensis* has a less transverse P^4 with short weak precingulum and no postcingulum and the protocone with its crests is higher.

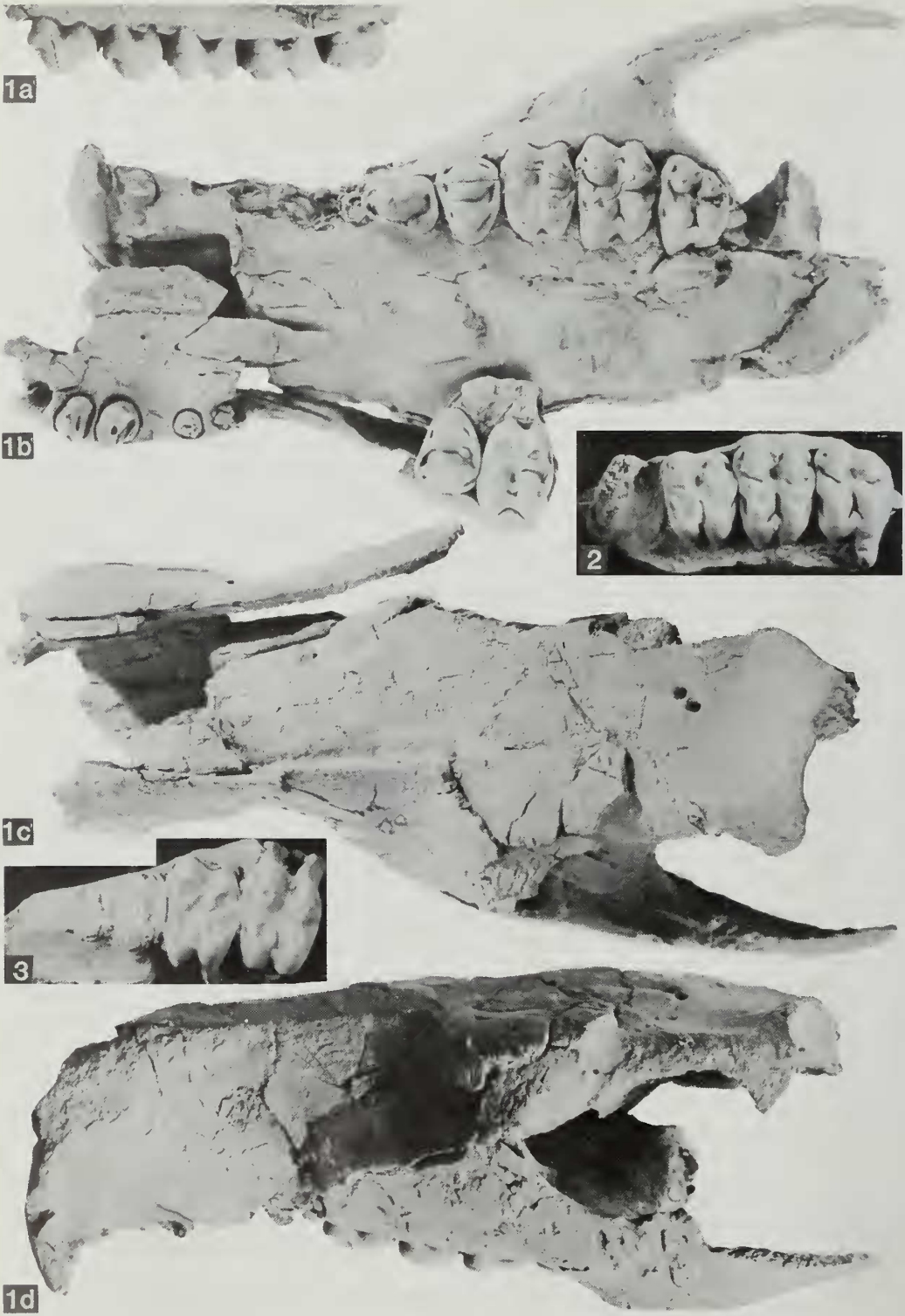
Molars. These resemble *C. minor*, *C. lacustris* and *C.* '*helveticus*' in the presence of a protolophule joining the paracone and in the premetaconule crista tending to form a prominent central accessory conule and to join the metacone. Buccal cingula are restricted to between the paracone and metacone and near the parastyle and metastyle. There is a very small mesostyle on M^2 and a larger one on M^3 associated with buccal flexing of the centrocrista. These cingular features show much variation in *C. minor* from Lamandine, three specimens including the holotype having a strong cingulum round the metacone, one having a complete buccal cingulum and two others being like the Barton specimen. The fact that the Mémerlein *C. lacustris* upper molars have the buccal cingulum continuous round the metacone is thus not considered a taxonomic difference either from the Barton specimen or from specimens of *C. minor* from the type locality. Similar variation occurs in *C.* '*helveticus*' but no specimens appear to exist with a complete buccal cingulum.

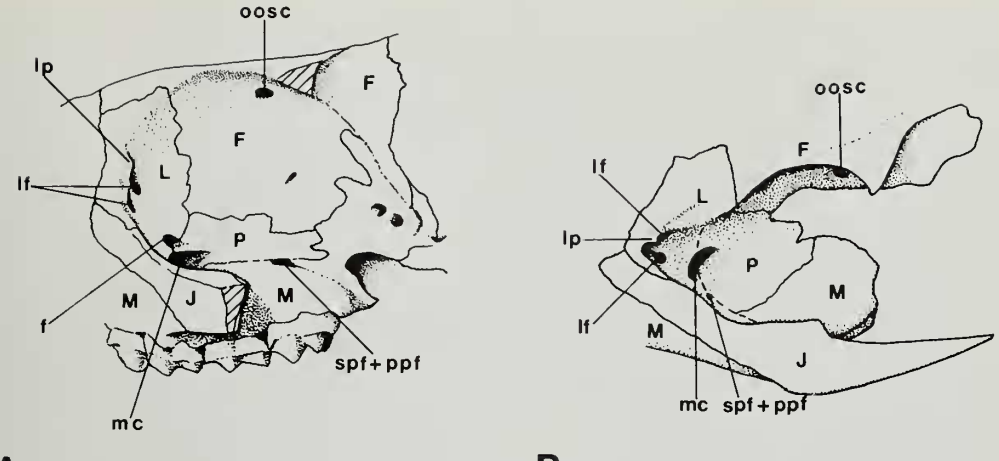
Osteology. The cranium is smaller than, but otherwise very similar to, that of *C. lacustris* from Mémerlein, which has been extensively described and figured by Pearson (1927). Only those features which are new or differ from this species are described here.

Recognition of sutures and orbital foramina is made difficult by surface erosion and crushing. Text-figs 58–59 attempt to show these and other features and reconstruct the cranial shape. I have relied heavily on the well-preserved cranium of *A. saturninum* (MNHN Qu16366, holotype of *Leptacotherulum cadurcense*) to guide interpretation of sutures and foramina (Text-fig. 58A; see also Russell 1964: 263, text-fig. 57).

The left frontal preserves twinned supraorbital foramina, probably an individual character (cf. Sisson & Grossman 1953: 137, for *Bos taurus* L.). Their position above M^3 is like *C. lacustris* (see Pearson 1927). In the crania of all other species of *Cebochoerus* and *Acotherulum*, where this feature is known, they are above M^2 (viz. *C.* aff. *fontensis*, *C. robiacensis*, *A. saturninum* and *A. quercyi*).

Immediately behind the postorbital process the anterior (frontal) edge of the temporal fossa


1a
1b
2
1c
3
1d



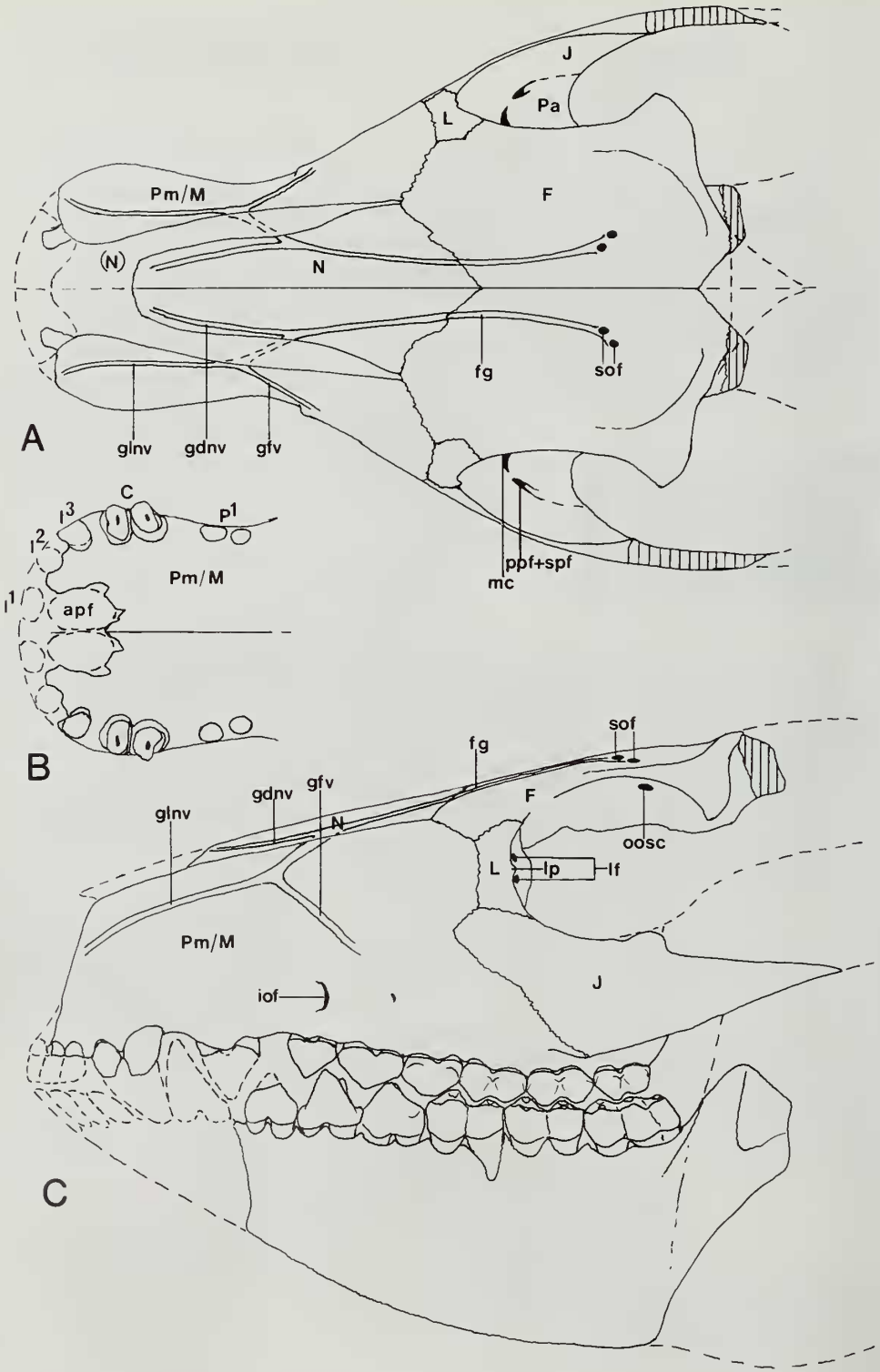
Text-figure 58 Left orbital regions of A, *Acotherulum saturninum* Gervais (holotype of *Leptacotherulum cadurcense* Filhol) from the Phosphorites du Quercy (MNHN Qu16366) (right side reversed); and B, *Cebochoerus minor* Gervais from Bed C, Barton Clay, Barton Cliff (M26649). Both × 1·3. Abbreviations: F = frontal; f = fossa (?for origin of the ventral oblique muscle of eyeball); J = jugal; L = lacrymal; lf = lacrymal foramen; lp = lacrymal process; M = maxilla; mc = maxillary canal; oosc = orbital opening of supraorbital canal; P = palatine; ppf = postpalatine foramen; spf = sphenopalatine foramen.

has a transverse orientation. This is like all cranially known *Acotherulum* and *Cebochoerus* species except *C. lacustris*, where the frontal extends backwards from the postorbital process almost to a position vertically above the anterior edge of the squamosal (see Pearson 1927: text-fig. 22).

The anterior edge of the very shallow narial incision is preserved on the right premaxilla and on a tiny fragment of the right nasal. The configuration is very similar to that of *C. lacustris*, the only other cebochoerid where this part is known. The maxillary–premaxillary suture is not visible, apparently owing to fusion of these bones. Part of the edge of the right anterior palatine foramen is preserved, a feature covered by matrix/plaster on the *C. lacustris* cranium and unknown in any other specimen.

Significance of the P^3 characters in *C. minor*. The difference in protocone size between *C. minor* on the one hand and *C. 'helveticus'* and *C. lacustris* on the other is not taken here to be a specific character because of variation in the relevant occluding parts of P_4s of *C. minor*: in particular two jaws with lightly worn premolars, one from Lamandine (MNHN Qu67) and another with no detailed provenance but of very similar preservation (MNHN Qu79). In Qu79 the P_4 paracristid has a doubly concave buccal phase facet which would have occluded with a P^3 postparacrista with small metacone. A lingual phase facet is present near the tip of the protoconid, sloping mesiolingually at a shallow angle; this would have made contact with a small distolingual P^3 protocone such as occurs on the Barton cranium. Qu67 (Filhol 1877*b*: pl. 14, figs 288–290) has a similar but more worn and flatter buccal phase facet on the P_4

Plate 31 Light macrographs of *Cebochoerus minor* Gervais, × 1·6. Fig. 1a–d, partial cranium (M26649) from Barton Cliff; in lateral (a, left cheek tooth row only), ventral (b), dorsal (c) and left dorsolateral (d) views. Fig. 2, holotype left M^{1-3} (MNHN Qu60b) from Lamandine, in occlusal view. Fig. 3, right M^{1-2} with roots of P^{3-4} (reversed) (MNHN Qu71) from Lamandine, in occlusal view. See p. 391.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paracristid and another buccal phase facet near the tip of the large metaconid caused by contact with the postprotocrista of a P^3. Also on the paracristid but lingual to the buccal phase facet is a long lingual phase facet sloping steeply in a mesial direction. This would have been caused by a larger, less distal P^3 protocone. Whether this protocone would resemble that of *C. lacustris* or *C.* aff. *fontensis* remains unclear, but P^3 and P_{3-4} appear to be rather variable teeth in *C. minor*. Similar potential variation is demonstrated by two Mémerlein mandibles, one belonging to the cranium and an immature one consisting mainly of symphysis (M32172) with an unerupted P_3. In the latter, P_3 has a prominent metaconid distolingual to the protoconid, whereas in the former the metaconid is smaller and distal to the protoconid.

DISTINGUISHING FEATURES OF *C. minor*, *C.* '*helveticus*' AND *C. lacustris*. The only observable difference between *C. minor* and *C. lacustris*, apart from size, is in the anterior edge of the temporal fossa. *C.* '*helveticus*' is intermediate in size between the two, no cranial characters are known and it resembles *C. lacustris* in its partly unreliable P^3.

Sudre's (1978*b*: 75–76) diagnosis and discussion of *C. lacustris* does not help as it is mainly concerned with distinguishing it from '*G.*' *minor*, not *C. helveticus*. Recorded contemporaneity of *C. minor* and *C. lacustris* applies to the type locality of the former (Lamandine) and relies on Stehlin's (1908: 742) determination of specimens in Montauban and Munich museums. The quoted measurements indeed compare well with those of the Mémerlein skull of *C. lacustris*. The measurements which Sudre (1978*b*: 75) quoted for the now lost holotype maxilla of *C. lacustris* (8 mm for each of the three molars) are taken from Gervais' (1876: 48) type description of *C. minor*, not *C. lacustris*. Therefore his maxilla from Fons 6 and the tooth from Sosis can reasonably be reidentified as *C. minor*. Gervais (1859: 197–198, text-fig. 20), in the first meaningful description of the holotype of *C. lacustris*, gave M^{1-3} length as 27 mm, width of M^1 as 21 mm (which must be an error) and P^3–M^3 length as 41 mm.

Text-fig. 57, p. 392, shows length and width of upper molars for these three species. It shows the Barton cranium to plot easily within the range of variation of the type assemblage of *C. minor*. The known specimens of *C.* '*helveticus*' (type assemblage only) overlap with *C. minor* and approach *C. lacustris*. There are several possible conclusions on the status of *C.* '*helveticus*' from these data: 1, it consists of a mixed assemblage of *C. minor* and *C. lacustris*; 2, it is a species distinct from either, differing in characters as yet unknown; or 3, it is conspecific with *C. minor*, representing a degreee of intraspecific variation resulting from geographical and/or stratigraphical differences. Text-fig. 60A is a cumulative graph of coefficients of variation for the measurements given in Text-fig. 57. A variable but low v for seven *C. minor* specimens from Lamandine is increased to 6·4 in length and 7·7 in width when *C.* '*helveticus*' measurements are added. These coefficients are still insufficient to demonstrate a specific separation of *C.* '*helveticus*' from *C. minor*. They support the choice of conclusion 3 above, although conclusion 2 can never be excluded. The addition of measurements of specimens from Sosis, Le Bretou, Fons 6 and Barton reduces the coefficient, but the addition of two specimens of *C. lacustris* raises it to a level which suggests that on size alone more than one species is now represented.

It is possible that speciation resulted from isolation during the Bartonian. Perhaps the Swiss and French assemblages gave rise to *C. lacustris* by slight size increase; English *C. minor* remained unchanged but spread to France and Spain after the end of the Bartonian.

Text-figure 59 Partial reconstruction of skull of *Cebochoerus minor* Gervais. Cranium based on M26649 from Bed C, Barton Clay, Barton Cliff; mandible on MNHN Qu67 from Lamandine. × 1·3. Abbreviations: apf = anterior palatine foramen; F = frontal; fg = frontal groove; gdnv = groove for dorsal nasal vein; gfv = groove for facial vein; glnv = groove for lateral nasal vein; iof = infraorbital foramen; J = jugal; L = lacrymal; lf = lacrymal foramen; lp = lacrymal process; M = maxilla; mc = maxillary canal; N = nasal; oosc = orbital opening of supraorbital canal; Pa = palatine; Pm = premaxilla; ppf = postpalatine foramen; sof = supraorbital foramina; spf = sphenopalatine foramen. A, dorsal view of cranium, B, ventral view of anterior end of palate and C, left lateral view of cranium and mandible.

Cebochoerus robiacensis Depéret 1917
(Pl. 32, figs 2, 4, 5; Text-fig. 60B)

v. *1977b* *Cebochoerus* cf. *ruetimeyeri* Stehlin; Hooker: 141.
v. *1980* *Cebochoerus* cf. *ruetimeyeri* Stehlin; Hooker & Insole: 44.

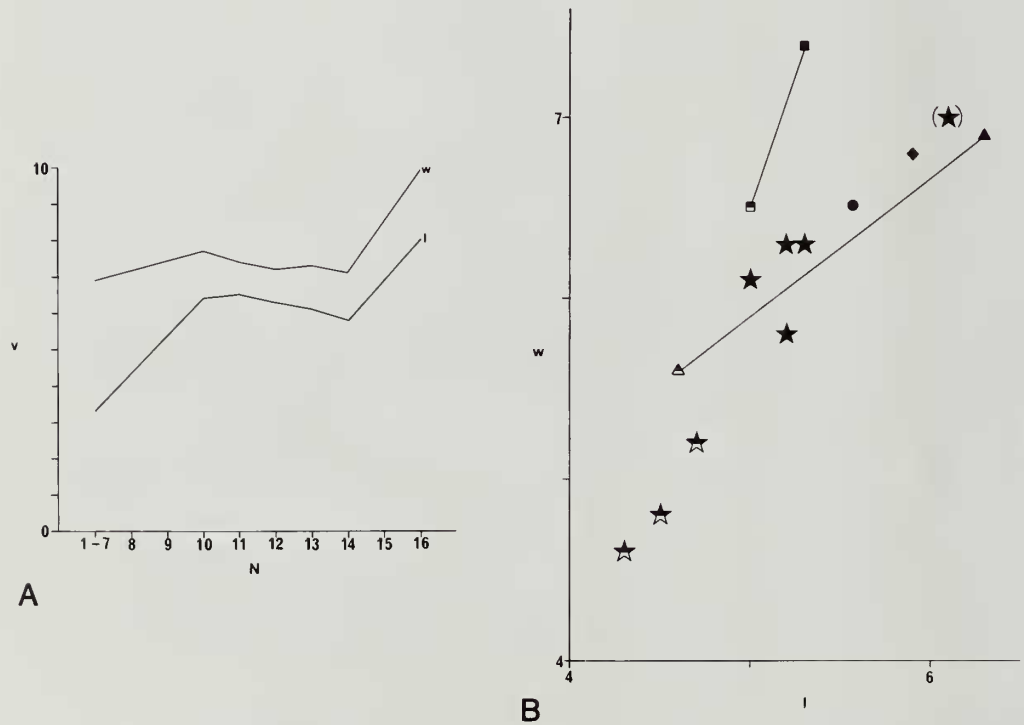
LECTOTYPE. Right maxillary fragment with M^{2-3} (NMB Rb52). Marinesian, Robiac (figured Stehlin 1908: text-fig. 109); selected Sudre, 1969*a*: 125.

RANGE. Marinesian, England and France.

MATERIAL. Right M^3 (M36803); right DP^4 (M37498); left $M_{1/2}$ (M37501); 2 right $M_{1/2}$ trigonid fragments (M36860, M37504); and possibly a distal fragment of left DP_4 (M37503).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Small *Cebochoerus* (mean length of M^1 = 5·3 mm). Upper molars with: protolophule not joining paracone; and lingual crown height > buccal crown height. P^4 width/length ratio 1·1. P^3 with protocone lingual to paracone; and outline not narrowing mesially. P^2 with protocone. Supraorbital foramina above level of M^2. Frontals not extended posteriorly from postorbital processes.



Text-figure 60 A, cumulative curves of coefficients of variation for lengths and widths of M^1 of the *Cebochoerus minor/helveticus/lacustris* complex. 1–7 from Lamandine; 8–10 from Mormont; 11 from Sosis; 12 from Le Bretou; 13 from Fons 6; 14 from Barton; 15–16 from Souvignargues and Mémerlein. B, scatter diagram of length (l) against width (w) in P^4 and M^3 of *Cebochoerus robiacensis* Depéret and *Acotherulum campichii* (Pictet). △ = *C. robiacensis* from Lautrec (measured from cast); ◇ = *C. robiacensis* from Caylux; ○ = *C. robiacensis* from Robiac; □ = *A. campichii* from Mormont (measured from Stehlin 1908: pl. 14, fig. 6); ☆ = *C. robiacensis* and *A. campichii* from Creechbarrow. Symbols solid above = P^4; completely solid = M^3. Measurements in millimetres. Lines join teeth of one individual.

DESCRIPTION AND DISCUSSION. Sudre (1978*b*: 66) synonymized this species with *Acotherulum campichii* (Pictet) comb. nov. (p. 400), which he referred to the genus *Cebochoerus*. In discussing his identification of specimens as '*C.*' *campichii*, he noted that the maxilla from Mormont figured by Stehlin (1908: pl. 14, fig. 6) differed from the Robiac material in having broader P^4 and shorter M^3. He considered that these characters had no evolutionary value and constituted simply individual variation. Three more characters – small upper molar paraconule, mesiolingual P^4 protocone and weak mesial and distal cheek tooth cingula and crests – also distinguish the Mormont maxilla from the Robiac material. These last characters are constant for three P^4s and five upper molars from Creechbarrow. These specimens are thus referred to *A. campichii* (see p. 400) and demonstrate the taxonomic importance of these characters in the distinction of *C. robiacensis* from *A. campichii*.

The Creechbarrow M^3 (M36803, Pl. 32, fig. 4) can be distinguished further from those of *A. campichii* by being slightly larger and by the mesial margin being convex, because of the bulging paraconule. Its paracone is broken buccally but a buccal cingulum appears to have continued round this cusp from the metaconal region. The cingula of the lectotype, according to Stehlin's figure, have a similar extent; but further specimens from Robiac, Lautrec (Sudre 1978*b*: text-pl. 6, figs 1, 3) and Caylux (Pl. 32, fig. 8) have weaker buccal cingula, showing this to be a variable feature.

The DP^4 (Pl. 32, fig. 2) has thinner enamel than the M^3; an almost complete strong buccal cingulum, only slightly interrupted at the paracone; shallow concave valleys; and a strong postprotocrista which almost joins the premetaconule crista.

The lower molars can be distinguished from those of *A. campichii* by having the mesial and distal crests of protoconid and hypoconid meeting at acute angles. M37501 has a mesoconid but this is a variable feature, common in *Cebochoerus*, less common in *Acotherulum*. It also has the hypoconulid at a more longitudinal orientation to the postcristid; this is another feature which is variable but more common in *Cebochoerus* than *Acotherulum* (see Pl. 32, figs 5b, 6b). The character of the hypoconulid is also visible on the DP_4 fragment.

C. robiacensis has not previously been given a character diagnosis. Authors have tended only to seek recognition of it either as the ancestor of *C. minor* (Depéret 1917: 113) or the descendant of '*C.*' *suillus* (Stehlin 1908: 745). Although relatively easily distinguishable from *A. campichii*, as shown above, it is less easily separated from the Auversian *C. ruetimeyeri*. *C. ruetimeyeri* is usually slightly larger and tends to have stronger buccal and lingual cingular developments, but there is much overlap. The most reliable difference appears to be lower lingual crown height of upper molars in *C. ruetimeyeri*, this being approximately equal to the buccal crown height.

Genus *ACOTHERULUM* Gervais 1850

[incl. *Metadichobune* and *Leptacotherulum* Filhol 1877*a*, *Cebochoerus* (*Gervachoerus*) Sudre 1978*b* in part, and ?*Moiachoerus* Golpe-Posse 1972]

TYPE SPECIES. *A. saturninum* Gervais 1850. Ludian; La Débruge, Vaucluse, France (?including *Leptacotherulum cadurcense* Filhol 1877*a*).

INCLUDED SPECIES. *A. quercyi* (Stehlin 1908) Sudre 1978*b*; *A. campichii* (Pictet 1857) comb. nov.; *A. pumilum* (Stehlin 1908) Sudre 1978*b*; *A.* sp. (Bembridge Limestone).

RANGE. Marinesian to late Ludian, England; Marinesian to Ludian, France and Switzerland; Ludian, Spain; and early Stampian, Belgium.

EMENDED DIAGNOSIS. $P\frac{1}{1}$ large and caniniform; C_1 incisiform. Upper cheek teeth with weak mesial and distal cingula and crests. Upper molars with: small paraconule; lingual crown height > buccal crown height; fused or unfused lingual roots; postprotocrista restricted to distal wall of protocone; protolophule not joining paracone. P^4 protocone mesiolingual to paracone. P^3 protocone lingual to paracone; P^3 outline narrowing mesially. P^2 protocone absent. Lower molars with angles of protoconid and hypoconid crests right-angled to obtuse. Supraorbital foramina above level of M^2. Adult horizontal mandibular ramus scarcely deeper below M_3 than below P_2.

Acotherulum campichii (Pictet 1857) comb. nov.
(Pl. 32, figs 1, 3, 6, 7; Text-fig. 60B)

v. *1977b Cebochoerus* cf. *campichii* (Pictet) Stehlin; Hooker: 141.
v. *1980 Cebochoerus* cf. *campichii* (Pictet) Stehlin; Hooker & Insole: 44.

Holotype. Right mandibular ramus with P_1–M_2. Sidérolithique; Mormont, Canton Vaud, Switzerland (figured Pictet 1857: pl. 4, figs 5–9), now lost according to Stehlin (1908: 729). De la Harpe (1869: 466) recorded the species (as *Dichobune Campichii*) from only one of the Mormont localities – Gare d'Eclépens, so it can be concluded that the missing holotype came from there.

Range. Marinesian; England, France and Switzerland.

Material. Three right P^4s (M36191, M36807, M37497); two left M^3s (M36802, M37499); two right M^3s (M36804, M37500); mesial fragment of right upper molar (M36805); left $M_{1/2}$ (M37502); and left M_3 lacking trigonid (M36183).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Emended diagnosis. Medium–small *Acotherulum* (length of $M^1 = 5{\cdot}6$ mm). Upper molar lingual roots fused. $M_{1/2}$ more than half as wide as long.

Description. Size appears to be slightly less than in the Mormont material (see Text-fig. 60B and Stehlin 1908: 731; pl. 14, fig. 6).

P^4: M37497 is very worn and shows few detailed features. M36191 shows a small metacone immediately behind the paracone. M36807 has no metacone. Both M36191 and M37497 have suggestions of a distal accessory conule and M37497 also a paraconule. In M37497, distinction from *C. robiacensis* can still be made by the position of the protocone and the low mesial and distal crests and cingula which have hardly been affected by the heavy wear which has removed most of the paracone and protocone (cf. Sudre 1978*b*: text-pl. 6, figs 1b, 3).

M^3: Variation is mainly in outline shape and distribution of cingula. The terminal bulge of the outline is midway along the metacingulum in M37499 and M36804 and is in the metastylar region in M36802 and M37500. The cingulum is continuous round the metacone in M37499, M36804 and M36802. In M37500, the precingulum does not extend as far lingually as in the other three. M36804 is the only specimen with even the slightest development of a postcingulum. M36802 and M36804 each have a very small accessory conule. This is absent in M37500 and the area is too worn to tell in M37499. All have small paraconules, which distinguish them from *C. robiacensis* from the same locality (see p. 398).

$M_{1/2}$: M37502 is significantly narrower relatively than the same tooth attributed herein to *C. robiacensis*; it has no mesoconid; the paracristid is bent asymmetrically; the hypoconulid merges gradually with the postcristid; and the tooth as a whole appears less robust.

M_3: What remains of M36183 is fairly worn. It appears to have been relatively narrow; there is a lingual accessory conule between the entoconid and hypoconulid; and the cingula are weak. Size and the accessory conule are more consistent with attribution to *A. campichii* than to *C. robiacensis*.

Phylogenetic implications within the Cebochoeridae. Table 34 compares characters of the various species of *Cebochoerus* and *Acotherulum*. Primitive versus advanced states have been

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Plate 32 Light macrographs of cheek teeth of *Cebochoerus* and *Acotherulum*, ×5. Views are buccal (a), occlusal (b or unsuffixed) and lingual (c).

Figs 1, 3, 6, 7 *Acotherulum campichii* (Pictet) from Creechbarrow. Fig. 1a, b, right P^4 (reversed) (M36807). Fig. 3a, b, right M^3 (reversed) (M37500). Fig. 6a–c, left $M_{1/2}$ (M37502). Fig. 7a–c, left M_3 talonid fragment (M36183). See above.

Figs 2, 4, 5 *Cebochoerus robiacensis* Depéret from Creechbarrow. Fig. 2a, b, right DP^4 (reversed) (M37498). Fig. 4a, b, right M^3 (reversed) (M36803). Fig. 5a–c, left $M_{1/2}$ (M37501). See p. 398.

Fig. 8 *Cebochoerus robiacensis* Depéret from Caylux. Right maxilla with M^{1-3} (reversed) (M7528).

1a

2a

3a

4a

1b

2b

3b

4b

5a

6a

7a

5b

6b

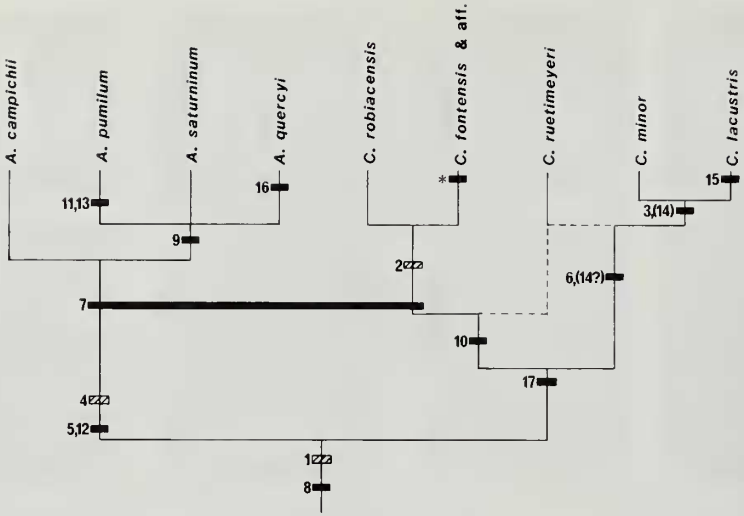
7b

5c

6c

7c

8



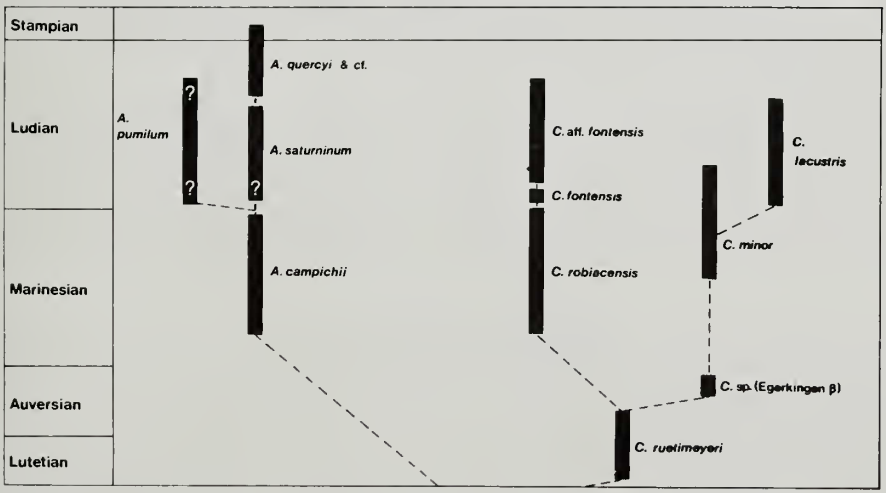
Text-figure 61 Cladogram of species of *Acotherulum* and *Cebochoerus*. This is the most parsimonious possibility. Character 7 is apparently the only parallelism. Because of the incompleteness of certain species, some of their character states are unknown (see Table 34 opposite). Two of these characters (15 and 16) are each only known in a single species, unknown in closely related species and define terminal dichotomies. Their occurrence in the poorly-known, less related forms is unlikely, but if shown to occur they would be incongruent with other characters and would thus be parallelisms. Most of the other incompletely known characters are more fundamental and are shown hatched. Character 2 is poorly known in *Acotherulum* but is tentatively considered consistently primitive, as in its advanced state it is distinctive of only two species of *Cebochoerus*. The problems posed by characters 1, 3 and 4 could be overcome by excluding the very poorly known *A. pumilum* from the cladogram. *C. ruetimeyeri* is variable for two characters which are constant but different in the two terminal groups of *Cebochoerus*. Using only the advanced states of these characters, *C. ruetimeyeri* can be related equally to the *C. robiacensis/fontensis* group or to the *C. minor/lacustris* group, unless in the future it is found to have the advanced state for character 14. This would relate it more to the latter group, but it remains otherwise totally primitive within the genus *Cebochoerus*. Lack of knowledge of certain characters renders the cladogram very tentative, but it may be hoped the gaps will be filled by the anterior dentition and skull parts eventually becoming known for the incomplete species. By applying the cladogram to the occurrence of the species in the stratigraphical record, the phylogeny shown in Text-fig. 62 is produced. (* = greater size.)

calculated by outgroup comparison with the rest of the Dichobunoidea, except character 14, which was by ingroup comparison as it is relatively poorly known outside the Cebochoeridae. *C. suillus* (Gervais 1852) Stehlin 1908, *C. dawsoni* Sudre 1978*b* and *C. jaegeri* Sudre 1978*b* are omitted since distinctive characters such as small premolariform P_1 and upper molar post-protocrista joining metaconule indicate that a new genus is required to include them.

One way of displaying these character distributions is in the form of a cladogram (Text-fig. 61). *Cebochoerus ruetimeyeri* shares incipient development of advanced character 10 with the *C. robiacensis/fontensis* group and of advanced character 6 with the *C. minor/lacustris* group. It is otherwise primitive with respect to both, which makes *C. ruetimeyeri* from Egerkingen α a good candidate for their common ancestry. These groups correspond partially to Sudre's subgenera *Gervachoerus* and *Cebochoerus* respectively, but are much more restricted. A maxilla from Egerkingen β was referred to *C. ruetimeyeri* by Stehlin (1908: pl. 14, fig. 55). It is intermediate between the latter and *C. minor* in size and has an upper molar protolophule joining the paracone, as in *C. minor*. A phylogeny is proposed in Text-fig. 62.

Table 34 Characters and character states of species in the genera *Cebochoerus* and *Acotherulum*. Characters are estimated as primitive (−) or advanced (+) based on outgroup comparison with the rest of the Dichobunoidea. Lack of information on a character indicated by '?'.

Character	State: Primitive	State: Advanced	*A. campichii*	*A. saturninum*	*A. quercyi*	*A. pumilum*	*C. fontensis* & aff.	*C. robiacensis*	*C. ruetimeyeri*	*C. minor*	*C. lacustris*
1. $P\frac{1}{1}$ caniniform	no	yes	+	+	+	?+	+	+	+	+	+
2. P^2 protocone	absent	present	?	?	−	?	+	+	−	−	−
3. P^3 protocone position regarding paracone	lingual	distolingual	−	−	−	?−	−	−	−	+	+
4. P^4 protocone position regarding paracone	lingual	mesiolingual	+	+	+	?+	−	−	−	−	−
5. Upper molar paraconule	large	small	+	+	+	+	−	−	−	−	−
6. Upper molar protolophule joining paracone	no	yes	−	−	−	−	−	−	+/−	+	+
7. Upper molar lingual: buccal crown height	=	>1	+	+	+	+	+	+	−	−	−
8. Upper molar postprotocrista separate from metaconule	no	yes	+	+	+	+	+	+	+	+	+
9. Upper molar lingual roots	fused	separate	−	+	+	+	−	−	−	−	−
10. M^1/P^4 size ratio	high	low	−	−	−	−	+	+	+/−	−	−
11. P_4 paraconid high	no	yes	−	−	−	+	−	−	−	−	−
12. Angle of lower molar protoconid and hypoconid crests	acute	obtuse	+	+	+	+	−	−	−	−	−
13. Lower cheek teeth	wide	narrow	−	−	−	+	−	−	−	−	−
14. Supraorbital foramina above M^2 or M^3	M^2	M^3	?	−	−	?	−	−	?	+	+
15. Frontal projects behind postorbital process	no	yes	?	−	−	?	−	−	?	−	+
16. Jugal	shallow	deep	?	−	+	?	−	−	?	−	−
17. Horizontal mandibular ramus	shallow	deep	−	−	−	?−	+	+	+	+	+



Text-figure 62 Proposed phylogeny of *Acotherulum* and *Cebochoerus* in the Eocene of Europe; based on the cladogram of Text-fig. 61 and stratigraphical occurrence.

Suborder **ANCODONTA** Matthew 1929*b*

Superfamily **ANTHRACOTHERIOIDEA** Gill 1872

Note that the Choeropotamidae are included here, not in the Dichobunoidea. Their differences from the Cebochoeridae are fundamental and I follow Stehlin (1908) in considering the family close to *Haplobunodon*.

Family **HAPLOBUNODONTIDAE** Pilgrim 1941 (*sensu* Sudre 1978*b*)

TYPE GENUS. *Haplobunodon* Depéret 1908.

INCLUDED GENERA. *Rhagatherium* Pictet 1857; *Amphirhagatherium* Depéret 1908; *Lophiobunodon* Depéret 1908; *Anthracobunodon* Heller 1934; *Masillabune* Tobien 1980; ?*Thaumastognathus* Filhol 1890*a*.

RANGE. Early Lutetian to late Ludian, Europe.

DIAGNOSIS. See Sudre (1978*b*: 90).

Genus ***HAPLOBUNODON*** Depéret 1908

[The main early generic and specific synonymies are complex and are dealt with by Stehlin (1908: 752–765)]

TYPE SPECIES. *H. lydekkeri* Stehlin 1908. Lower Headon Beds; Hordle Cliff, Hampshire. Nomenclatural background is given by Stehlin (1908: 752–754).

INCLUDED SPECIES. *H. solodurense* Stehlin 1908; *H. muelleri* (Rütimeyer 1862) Stehlin 1908; ?*H. ruetimeyeri* (Pavlow 1900) Stehlin 1908; and *H. venatorum* sp. nov.

RANGE. Late Lutetian to Ludian, Switzerland; Marinesian to early Ludian, France and England.

EMENDED DIAGNOSIS. $P\frac{1}{1}$ present to absent. No diastema between P_2 and P_3. P^{3-4} with outline as an isosceles triangle and without metacone. Upper molars semibunodont with mesostyles less than half the height of the paracone; paraconule smaller than protocone and not separated from it by deep fissure; premetaconule crista short, often joined to protocone. M^3 distal edge straight. P_{3-4} without hypoconid. P_4 often with large paraconid. Lower preultimate molars with postcristid joining hypoconulid usually independently of entoconid. [The otic region has been described by Pearson (1927: 438–440) for *H. lydekkeri*, but for no other haplobunodontid].

DISCUSSION. From Pavlow's (1900: pl. 5, figs 6–7) figures (fig. 6 reproduced by Stehlin, 1908: 773, text-fig. 112), *H. ruetimeyeri*, with large mesostyle, large paraconule and strongly oblique buccal edge distal to the mesostyle, fits Sudre's (1978*b*: 94–99; pl. 4, figs 7–8; pl. 5, fig. 5) concept of *Anthracobunodon* better than *Haplobunodon*. It could even be conspecific with *A. louisi* Sudre 1978*b* from Grisolles. Moreover, from outline shape and cusp pattern, the teeth in Pavlow's fig. 6 are more likely to be DP^4–M^1 than M^{1-2}.

Haplobunodon venatorum sp. nov.

(Pl. 33, figs 1–5; Pl. 34, figs 1–4; Text-figs 63–64; Table 35)

v. *1977b Haplobunodon* sp.; Hooker: 141.
vp. *1980 Haplobunodon* spp.; Hooker & Insole: 44.

NAME. Latin, 'of the hunters', in allusion to the remains of a Mediaeval hunting lodge on the summit of Creechbarrow.

HOLOTYPE. Right P_4, M37540. Pl. 34, fig. 2.

PARATYPES. Two right P^4s, one fragmentary (M37712, M37528); right M^{1-2} associated (M37529); two fragmentary $M^{1/2}$s (M37530, M37713); two left M^3s (M37531–2); right M^3 (M37533); three fragmentary upper molars (M37535–7); left P_4 (broken)–M_2 (broken) (M37716); right P_3 (M37539); right P_4 (M37541); right $M_{1/2}$ (M37542); fragment of right mandibular ramus with M_3 (M37544); three left M_3s, all lacking trigonid (M37545, M37714–5); and right lower molar fragment (M37543).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DIAGNOSIS. Large *Haplobunodon* (length of M^1 = 8·6 mm). P^4 broader than long, subtriangular in outline, with large protocone and strong ectocingulum and pre- and post-cingula. P_3 with metaconid and trifurcating postprotocristid. P_4 more than half as broad as long with metaconid and small entoconid present; and paraconid subequal in height to metaconid. Horizontal mandibular ramus not deepening beneath M_{1-3}.

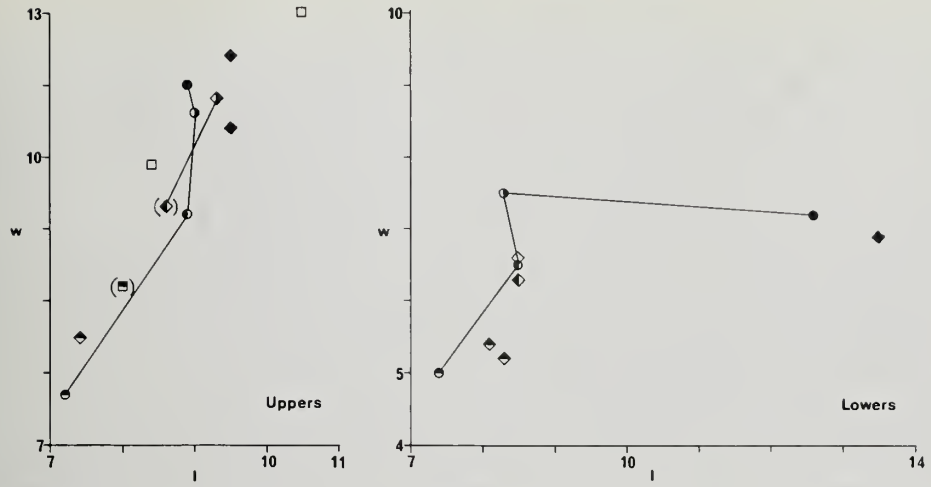
DIFFERENTIAL DIAGNOSIS. *H. muelleri* is much smaller and has a mandibular ramus deepening from M_{1-3}; P_{3-4} are unknown. *H. lydekkeri* is slightly smaller; has a P^4 with an equilateral triangular outline, a smaller protocone, weaker ectocingulum and no pre- and post-cingula; a P_3 without metaconid and with single postprotocristid; and a P_4 with a large metaconid subequal with protoconid and a smaller paraconid. *H. solodurense* is slightly smaller, has a P_3 without a metaconid and a narrower P_4 with a paraconid but no metaconid or entoconid.

Table 35 Length (l) and mesial (w_1) and distal (w_2) width measurements of *Haplobunodon venatorum* from Creechbarrow. Two width measurements are only given for lower molariform teeth. Measurements in millimetres.

No.	Tooth	l	w_1		w_2
M37712	RP^4	7·4		8·5	
M37529	RM^1	8·6		(10·3)	
M37529	RM^2	9·3		11·8	
M37532	LM^3	9·6		–	
M37531	LM^3	9·5		12·4	
M37533	RM^3	9·5		11·4	
M37716	LP_4	–		5·7	
M37716	LM_1	8·5	6·2		6·3
M37716	LM_2	–	7·9		–
M37539	RP_3	–		3·8	
M37540	RP_4	8·1		5·4	
M37541	RP_4	8·3		5·2	
M37542	$RM_{1/2}$	8·5	6·1		6·6
M37544	RM_3	13·5	7·9		6·9
M37545	LM_3	–	–		6·2
M37714	LM_3	–	–		6·6
M37715	LM_3	–	–		7·2
M37543	$RM_{1/2/3}$	–	6·7		–

DESCRIPTION. P^4: M37712 is quite worn. The cingula are faintly papillate. The ectocingulum, though strong, is interrupted between the midpoint on the paracone and the extensively crested parastyle. A small area of exposed dentine on the postparacrista indicates the presence of a tiny metacone. Its presence or absence in this state is intraspecifically variable in *H. muelleri* (see Stehlin 1910*b*: pl. 17, figs 35, 37). There is a worn swelling midway along the distal cingulum, which may have once been a small metaconule. There is a separation between this point and the postprotocrista which stops short, joining neither distal cingulum nor postparacrista.

1a
2a
3a
4a
5a
1b
2b
3b
4b
5b
5c
6a
6b
7a
7b



Text-figure 63 Scatter diagrams of length (l) against width (w) in upper and lower cheek teeth of species of *Haplobunodon*. Measurements in millimetres. Width of lower molariform teeth is talonid width. ◇ = *H. venatorum* sp. nov. from Creechbarrow; □ = *H.* aff. *venatorum* from Mormont; ○ = *H. lydekkeri* Stehlin from Hordle Cliff. Symbols solid above = P4; solid on left = M1; solid on right = M2; completely solid = M3; outline = M1/2. Lines join teeth of one individual.

M37528 has all the distal half and the lingual edge broken away. It resembles M37712 in what remains of the cingula, although the parastyle appears more weakly crested and it is less worn. A very worn right P^4 of *Haplobunodon* from Mormont (LGM 9157: LM 797, figured Stehlin, 1908: pl. 13, fig. 36) resembles M37712 except in that it is slightly larger, has more papillate cingula and the ectocingulum is more continuous.

M^{1-2}: Two preultimate molars which were found in the same bag of matrix, and whose interstitial facets match (M37529) are the only ones identified with certainty as being either tooth. M^2 is larger than M^1 and less worn. The ectocingulum is so weak on M^2 that it is nearly missing (M^1 is abraded in this area). The lingual cingulum in both is restricted to a short stretch between the protocone and metaconule. M37713 is broken but almost unworn, has a small ?hypostyle at the distal end of the postmetaconule crista, an almost complete cingulum round the metaconule and a low ridge in the valley, between the protocone and metaconule, which may represent a prehypocrista. Of three $M^{1/2}$s of *Haplobunodon* from Mormont (figured Stehlin, 1908: pl. 13, figs 16, 36 and 41) the last has thin enamel and is low-crowned, and is thus here reidentified as a DP^4. Of the remaining two, LGM 9166: LM 852 is the same length but slightly broader than the M37529 M^1 and has an almost complete ectocingulum; and LGM 9146: LM 854 is larger in both dimensions than the M37529 M^2, has a complete papillate ectocingulum, a faint postcingulum and signs of a prehypocrista.

M^3: This tooth varies in outline shape from being like the M^{1-2}s (M37529) to distally attenuated (M37531). The lightly worn example, M37529, can be distinguished from M^{1-2}s in

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Plate 33 Light macrographs of cheek teeth of *Haplobunodon* and *Dacrytherium* from Creechbarrow, × 3. Figs 1a, 2a, 3a, 5a, 6a, 7a are buccal views. Figs 1b, 2b, 3b, 4a, 5b, 6b, 7b are occlusal views. Figs 4b, 5c are lingual views.

Figs 1–5 *Haplobunodon venatorum* sp. nov. Fig. 1a, b, right P^4 (reversed) (M37712). Fig. 2a, b, right M^{1-2} (reversed) (M37529). Fig. 3a, b, right M^3 (reversed) (M37533). Fig. 4a, b, right P_4 (reversed) (M37541). Fig. 5a–c, left M_3 talonid fragment (M37545). See p. 404.

Figs 6–7 *Dacrytherium elegans* (Filhol). Fig. 6a, b, right M^{1-3}, M^1 fragmentary (reversed) (M37717). Fig. 7a, b, left $M^{1/2}$ (M36814). See p. 410.

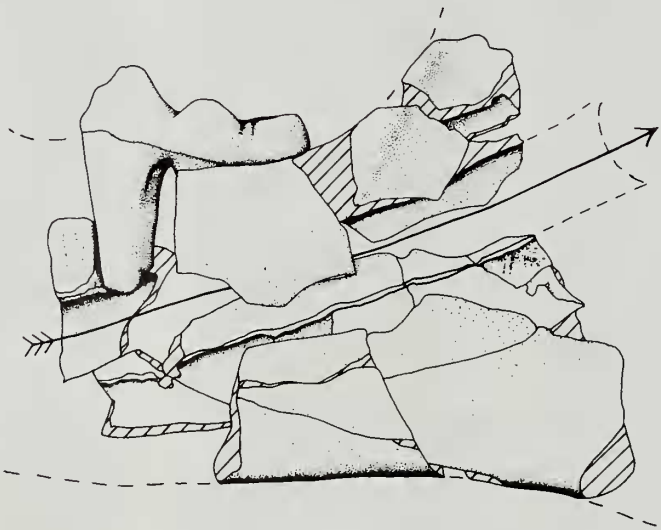
having the metacone lower than the paracone. M37531 also has a buccally salient metastyle. There is also variation in strength of the ectocingulum.

P_3: M37539 preserves only the distal half. Quite a large metaconid appears to have been present. The postprotocristid trifurcates, only the convex buccal limb reaching the distal tooth margin, where there is a small cusp. *H. solodurense* is similar but has no metaconid (Stehlin 1908: pl. 14, fig. 48; 1910*b*: pl. 20, figs 10, 62). *H. lydekkeri* (BM(NH) 29713) has no metaconid and only a single straight postprotocristid. The characters, inasmuch as they are constant for three specimens of *H. solodurense*, are considered to have specific value.

P_4: The two complete specimens both have very small entoconids but vary considerably in size of paraconid and metaconid although retaining the same relative sizes of these cusps. In the holotype (M37540), the paraconid is a large swollen cusp, slightly worn, but which was probably nearly as tall as the protoconid; the metaconid is a much narrower cusp; and the valley between this and the paraconid is very narrow. M37541 is more worn, but the metaconid forms a small distolingual bulge from the protoconid; the paraconid is much less inflated than on M37540; and the valley between the paraconid and metaconid is wide and very shallow. The M37716 P_4 has the paraconid broken away but has a small metaconid like M37541 and a slightly larger entoconid. Three P_4s of *H. solodurense* are constant for the specific differences from *H. venatorum* but vary in the size and position of the paraconid. In NMB Ef245 it is nearly as large as in M37541 but less lingual with respect to the protoconid (see Stehlin 1908: pl. 14, figs 35, 48; 1910*b*: pl. 20, fig. 55).

Lower molars: No tangible morphological differences between this and the other *Haplobunodon* species have been detected. In *H. venatorum* there is slight variation in size of the ectostylid. In M_3 there is also slight variation in the orientation of the mesial hypoconulid crest (longitudinal or oblique) and the position of its attachment mesially: midway between the hypoconid and entoconid in M37544–5 and M37715, or directly to the hypoconid by way of the postcristid in M37714.

Mandible: The M_3, M37544, is one of very few specimens found in the field during excavation work at Creechbarrow. It is associated with a shattered piece of mandibular ramus, which shows the configuration in the region of M_3 to have been like that of *H. lydekkeri* (see Text-fig. 64 and Cooper 1928: pl. 2, fig. 2) and *H. solodurense*.



Text-figure 64 Medial view of right mandibular fragment with M_3 of *Haplobunodon venatorum* sp. nov. (M37544) from Creechbarrow. Arrow indicates course of dental canal. × 2·3.

Discussion. Considering the intraspecific variation in the Creechbarrow assemblage, it is probable that most of the Mormont material is conspecific with it, although exact identity is not demonstrable. It will thus be referred to as *H.* aff. *venatorum.* Its age is considered to be Marinesian, based on one specimen labelled 'Eclépens' and none being labelled 'Entreroches'. The small upper molar from Entreroches (NMB Mt373; see Stehlin 1908: pl. 13, fig. 33; note that this is mislabelled in his plate legend as LM 853) is outside the range of size variation expected for *H. venatorum* and coincides closely with the size of *H. solodurense.*

The species morphologically closest to *H. venatorum* appears to be *H. solodurense* from the late Lutetian–Auversian of Egerkingen. It would be possible to derive the former from the latter by increase in overall size and also in premolar molarization, including the curious enlargement of the paraconid. However, there appear to be no temporal trends within the Egerkingen assemblages towards *H. venatorum.* Ludian *H. lydekkeri* appears more primitive in its paraconid and is unlikely to be the descendant of *H. venatorum. H. muelleri* appears to be more distantly related, as its jaw characters are not shared with the other three species. On this basis and on the presence of P_1 in *H. muelleri,* Stehlin (1910*b*: 1112) considered that it might eventually be placed in a separate genus. Unfortunately, all others except the type species are too incomplete to know whether they had $P\frac{1}{1}$.

Family ?**CHOEROPOTAMIDAE** Owen 1845 (*sensu* Sudre 1978*b*)

Genus ?***CHOEROPOTAMUS*** Cuvier 1822

?***Choeropotamus*** sp. indet.

vp. *1980 Choeropotamus* spp.; Hooker & Insole: 44.

Material. Fragment of right P^2? (M37563) and fragment of right P^4? (M37566).

Horizon and locality. Creechbarrow Limestone Formation, Creechbarrow.

Description. M37563 is broken mesially and distally, has a narrow wedge-shaped outline, one large cusp bordered by strong cingula and a very rugose surface. M37566 could be a distal fragment of P^4; it is more finely rugose than M37563, has a strong papillate cingulum continuous throughout the preserved edge and a slightly papillate crest which might be a postparacrista. Neither fragment fits any other taxon recorded from Creechbarrow but both resemble *Choeropotamus* in size, apparent bunodonty, enamel rugosity and probable outline. Size would correspond with *C. lautricensis* from the Marinesian of France. The identification is intended to be only very tentative, however. Both teeth are so fragmentary that no definite identification should be made even to ordinal level.

Superfamily **ANOPLOTHERIOIDEA** Bonaparte 1850
(rank emend. Romer 1966) (*sensu* Sudre 1978*b*)

Family **ANOPLOTHERIIDAE** Bonaparte 1850 (*sensu* Viret 1961)

Diagnosis. See Viret (1961: 935).

Subfamily **DACRYTHERIINAE** Depéret 1917
(rank emend. Viret 1961)

Type genus. *Dacrytherium* Filhol 1876*a.*

Included genera. *Catodontherium* Depéret 1908, *Leptotheridium* Stehlin 1910*b* and *Tapirulus* Gervais 1850.

Range. Middle Lutetian–early Stampian, Europe.

Diagnosis. See Viret (1961: 936).

Genus *DACRYTHERIUM* Filhol 1876*a*

[incl. *Plesidacrytherium* Filhol 1884; for more detailed synonymies see Stehlin, 1910*b*: 882–900.]

TYPE SPECIES. *D. cayluxi* Filhol 1876*a*. Early Ludian limestone; Lamandine, Quercy, France. Following Stehlin (1910*b*: 843) this species is almost universally synonymized by authors with *D. ovinum* (Owen 1857*b*), from the Lower Headon Beds of Hordle Cliff, Hampshire (not the Isle of Wight as originally stated by Owen, 1857*b*, and followed by Stehlin, 1910*b*, and Sudre, 1978*b*).

INCLUDED SPECIES. *D. saturnini* Stehlin 1910*b*; *D. priscum* Stehlin 1910*b*; *D. elegans* (Filhol 1884) Stehlin 1910*b*; and *D.* cf. *elegans*.

RANGE. Middle Lutetian to Ludian; England, France and Switzerland.

DIAGNOSIS. See Sudre (1978*b*: 110).

Dacrytherium elegans (Filhol 1884) Stehlin 1910*b*

(Pl. 33, figs 6–7; Text-fig. 65)

v. *1977b* *Dacrytherium* sp.; Hooker: 141.
v. *1980* *Dacrytherium* sp.; Hooker & Insole: 44.

HOLOTYPE. Cranial fragment with P^3–M^3. Early Ludian limestone; Lamandine-Haute, Quercy, France (Filhol 1884: 191–192; pl. 10, figs 5–6).

RANGE. Marinesian, England, France and Switzerland; early Ludian, France.

MATERIAL. Distal fragment of right P^3 (M37564); right M^1 (fragmentary)–M^3 (M37717); left $M^{1/2}$ (M36814); right lower canine? (M37548); left P_2 (M37718); and fragment of lower deciduous premolar? (M36197).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

EMENDED DIAGNOSIS (essentially following Stehlin's 1910*b* description). Small *Dacrytherium* (mean length of M^1 = 8·0 mm). Upper molars strongly dilambdodont, with mesostyles broadly looped. Preorbital fossa shallow and restricted in extent.

DISCUSSION. The important character of the preorbital fossa obviously cannot be recognized when only teeth or jaws are available. This is the case with the Creechbarrow material. The pre-Marinesian species *D. priscum* and *D.* cf. *elegans* can be excluded from consideration since they are less dilambdodont. The teeth of the remaining species, however, appear to be only separable on size (see Sudre 1978*b*: 110). Text-fig. 65 is a scatter diagram of length against width of various upper molars of strongly dilambdodont species (mainly from published measurements). The Creechbarrow molars fit well with *D. elegans* from both the type locality and Eclépens-Gare. There is overlap, especially of M^1, with the slightly smaller *D. saturnini*, which appears otherwise to differ only in low size increase from M^1 to M^3 and in low length and high width variation of M^1. This species, according to Stehlin (1910*b*: 929), has a deep preorbital fossa like *D. ovinum*, but the material used here for size comparison is from Ste Néboule (Sudre 1978*a*: 278), where no specimen with a preorbital fossa preserved is recorded.

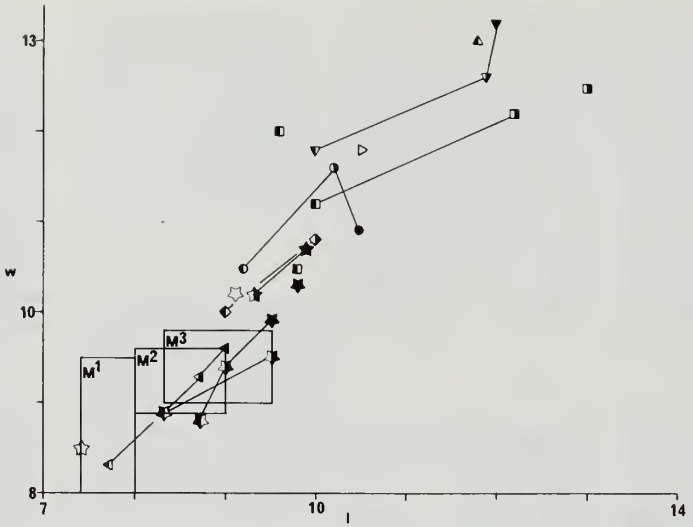
Plate 34 Light macrographs of cheek teeth of *Haplobunodon* and *Dichodon* from Creechbarrow, × 3. Views are buccal (a), occlusal (b or unsuffixed) and lingual (c).

Figs 1–4 *Haplobunodon venatorum* sp. nov. Fig. 1a–c, distal half of right P_3 (reversed) (M37539). Fig. 2a–c, **holotype** right P_4 (reversed) (M37540). Fig. 3a–c, left P_4 (paraconid broken), M_1 and trigonid fragment of M_2 (associated) (M37716). Fig. 4a–c, right M_3 (reversed) (M37544). See p. 404.

Fig. 5a–c *Dichodon* cf. *cervinus* (Owen). Left M_3 (hypoconulid broken) (M37549). See p. 413.

Fig. 6 *Dichodon* sp. indet. Distal fragment of left DP^2 (M37562). See p. 414.

1a
2a
3a
4a
1b
2b
3b
4b
4c
3c
2c
1c
5a
5b
5c
6



Text-figure 65 Scatter diagram of length (l) against width (w) in upper molars of species of *Dacrytherium*. Measurements in millimetres. Large rectangles delimit *D. saturnini* Stehlin from Ste Néboule (from Sudre 1978*a*: 278). ○ = Lamandine; □ = Fons 4; ◇ = Fons 5; △ = Perrière; ▽ = Euzet (these three localities from Sudre 1978*b*: tab. 11); ▷ = Eclépens B (from cast); (all *D. ovinum* (Owen) and *D.* sp. nov.?). ☆ = Creechbarrow; ☆ = Eclépens-Gare (from cast and Stehlin 1910*b*: pl. 16, fig. 10); ◁ = Lamandine (from Stehlin 1910*b*: text-fig. 158); (all *D. elegans* (Filhol), holotype from Lamandine). Symbols solid on left = M^1; solid on right = M^2; completely solid = M^3; outline = $M^{1/2}$. Lines join teeth of one individual.

The plots, especially of M^1s, in Text-fig. 65 also show a cluster larger than *D. ovinum* and discretely separate from it. Perhaps this represents an undescribed species. On morphological grounds, Stehlin's (1910*b*) '*D.* cf. *elegans*' from Egerkingen definitely requires a new specific name.

Suborder **TYLOPODA** Illiger 1811

Superfamily **XIPHODONTOIDEA** Flower 1884
(rank emend. Viret 1961)

Family **XIPHODONTIDAE** Flower 1884

TYPE GENUS. *Xiphodon* Cuvier 1822.

INCLUDED GENERA. *Paraxiphodon* Sudre 1978*b*, *Haplomeryx* Schlosser 1886 and *Dichodon* Owen 1848*a*.

RANGE. Late Lutetian–late Ludian, Europe.

DIAGNOSIS. See Sudre (1978*b*: 128).

Genus ***DICHODON*** Owen 1848*a*

TYPE SPECIES. *D. cuspidatus* Owen 1848*a*. Lower Headon Beds, Hordle Cliff, Hampshire.

INCLUDED SPECIES. *D. cervinus* (Owen 1841) Owen 1857*a*, *D. stehlini* Sudre 1973, *D. frohnstettensis* Meyer 1852, *D. simplex* Kowalevsky 1874, *D. subtilis* Stehlin 1910*b*, *D. cartieri* Rütimeyer 1891, *D. lugdunensis* Sudre 1972, *D. ruetimeyeri* Stehlin 1910*b*. See Stehlin (1910*b*), Depéret (1917), Dechaseaux (1965) and Sudre (1972, 1973, 1978*b*) for details of this genus. It is evident from the suffix of the name of the type species that Owen (1848*a*) intended *Dichodon* to be

masculine in gender, following that of the Greek original. Contrary to the common practice of authors, the suffixes of the other relevant adjectival species names listed above have been altered to make them agree.

RANGE. Late Lutetian–late Ludian, England, France, Switzerland and Spain.

DIAGNOSIS. See Stehlin (1910*b*: 1011–1017).

Dichodon cf. ***cervinus*** (Owen 1841) Owen 1857*a*
(Pl. 34, fig. 5)

vp. *1977b* *Dichodon* sp.; Hooker: 141.
vp. *1980* *Dichodon* sp.; Hooker & Insole: 45.

HOLOTYPE of *D. cervinus*. Left horizontal ramus containing M_{1-3}, with anterior edge of ascending ramus and detached piece of angular region (IGS GSM916). Shelly sandstone bed in Osborne Beds; Binstead, Isle of Wight. It has been figured by Pratt (1835: figs 1–2) and Owen (1846: 440, fig. 181).

RANGE of *D. cervinus*. Ludian, England, France, Switzerland and Spain; cf. Marinesian, England and Switzerland; aff. Marinesian, France.

DIAGNOSIS of *D. cervinus*. The species appears never to have been formally diagnosed. The best idea of its specific characters can be gained from the detailed descriptions of the type by Owen (1841, 1846) and of referred material by Stehlin (1910*b*: 1019–1021), Depéret (1917: 148–158; pl. 20) and Dechaseaux (1965).

MATERIAL. Left M_3, broken distally (M37549).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. A slight distal bend to the distobuccal wall of the hypoconid immediately preceding the distal truncation of the tooth indicates an M_3 (rather than an M_1 or M_2) from which the hypoconulid lobe and the distal part of the entoconid have been broken away.

Although it is not appropriate herein to rediagnose the two English *Dichodon* species (*D. cuspidatus* and *D. cervinus*), the principal differences between them are important to identification of the Creechbarrow specimen. In the former: 1, size is greater; 2, the upper molar parastyle, double mesostyle and metastyle are larger and more buccally salient; 3, the lower molar parastylid, metastylid, entoconulid and entostylid are larger and more lingually salient; and 4, the upper molar protocone and hypocone are as close together as the paracone and metacone instead of being wider apart (making the outline of the tooth taper lingually rather than be equiangular). Characters 2 and 3 are functionally linked by the occlusal relationships of the upper and lower teeth. Character 4 should result in the lower molar entoconid being smaller in *D. cuspidatus* than in *D. cervinus*, but I have not seen the necessary unworn specimens to verify this. It should be pointed out here that *D. stehlini* from La Débruge, which was thought to be derived from *D.* 'cf. *cervinus*' by Sudre (1973), was differentiated by him from *D. cuspidatus* on morphological features which appear to be variable within the type assemblage of the latter. In fact in character 4 above it is closer to *D. cuspidatus* than to *D. cervinus*. However, the upper molar from Robiac referred to *D.* aff. *cervinum* (Sudre 1969*a*: 135, fig. 18a) resembles *D. cuspidatus* in character 4.

M37549 fits *D. cervinus* in characters 1 and 3. Its talonid is narrower than its trigonid (7·2 mm for the trigonid, 6·7 mm for the talonid) and the length of the tooth minus the hypoconulid lobe is 8·9 mm. The same measurements of M_3 of the holotype of *D. cervinus* are 6·8 mm, 6·4 mm and 9·6 mm respectively. As in this specimen, the lingual stylar cuspids are relatively weak compared with those of *D. cuspidatus* (see Pl. 34, figs 5b–c).

Other details of M37549 are probably of an individual nature. The cristid obliqua extends deep into the valley between the metastylid and entoconulid, whereas the protocristid terminates more buccally. There is a short pillar-like ectostylid just lingual to the buccal tooth edge, with a thin enamel crest extending lingually a short distance from it.

Stehlin (1910*b*) recorded *D.* cf. *cervinus* from Mormont at both 'Station d'Eclépens' and 'Entreroches'. The Creechbarrow specimen tentatively supports a long range for this species from the Marinesian to the late Ludian.

Dichodon sp. indet.
(Pl. 34, fig. 6)

vp. *1977b* *Dichodon* sp.; Hooker: 141.
vp. *1980* *Dichodon* sp.; Hooker & Insole: 45.

MATERIAL. Distal fragment of left DP^2 (M37562); and left hypoconid fragment? (M37719).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. M37562 shows a metacone, swollen metastyle and a distal cingulum. There is no buccal cingulum on the part of the buccal edge preserved. In size it compares closely with that of two DP^2s of *D. cuspidatus* from the Lower Headon Beds of Hordle Cliff (BM(NH) 25248X and M25100). In morphology it is very close to the former (see Owen 1848*a*: pl. 4, figs 2, 3, 5), although it shows slightly more wear. M25100 shows no metastylar swelling and is overall a more strongly crested tooth.

M37719 is identified as an M_3 hypoconid as it appears broken mesially and distally at the junctions of adjacent tooth lobes. It is only slightly worn and gives a good idea of the crown height, which compares fairly well with similarly worn examples of *D. cuspidatus*. It differs, however, from M37549 in being intermediate in size between *D. cuspidatus* and *D. cervinus*.

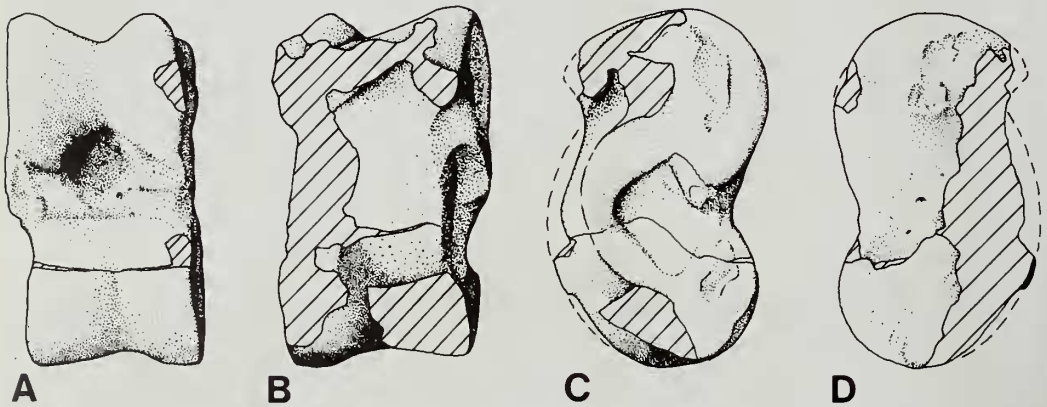
These two specimens indicate the presence of a species different from *D.* cf. *cervinus*, which may be related to *D. cuspidatus*. However, better material is needed.

Artiodactyla indet.
(Text-fig. 66)

MATERIAL. Right astragalus (M37567).

HORIZON AND LOCALITY. Creechbarrow Limestone Formation, Creechbarrow.

DESCRIPTION. Length is 9·9 mm, width of the tibial trochlea 5·0 mm and width of the trochleated head 4·7 mm. The bone is relatively straight-sided and elongate in dorsal or plantar views and it has deep dorsal and lateral cavities. The apparent shallowness of the tibial trochlea and absence of a ridge separating the cuboid and navicular facets on the trochleated head (the latter typically an advanced ruminant character) are probably the result of post-mortem abrasion.



Text-figure 66 Right astragalus of indeterminate artiodactyl (M37567) from Creechbarrow. Views: A, dorsal; B, plantar; C, lateral; D, medial. × 5.

The elongation and straightness together with the deep lateral cavity are characters found in the Xiphodontidae. The only xiphodont genus small enough is *Haplomeryx*, which is unknown from teeth at Creechbarrow. An astragalus of this genus from Euzet is poorly figured by Depéret (1917: pl. 19, figs 32–33). Creechbarrow artiodactyl taxa represented by teeth, of appropriate size for this astragalus, are *Hyperdichobune* sp. 1 (p. 376), *Cebochoerus robiacensis* (p. 398) and *Acotherulum campichii* (p. 400). Astragali are unknown for these genera. The only dichobunid astragali appear to be those attributed to *Protodichobune* by Teilhard (1922: pl. 3, figs 24–25) and *Messelobunodon* (Franzen 1981: 313). The former has a narrow neck and trochleated head only slightly more advanced than the primitive earliest Eocene diacodexids. The latter also has the trochleated head narrower than the tibial trochlea.

The specimen must remain indeterminate below ordinal level but there is a possibility that it may eventually prove to belong to one of the small cebochoerids in the fauna.

Correlation

Range of the Bartonian in England

Concepts of the stage. Mayer-Eymar (1857) originally based his Bartonian Stage on successions in the Hampshire, Paris and Belgian basins. He later (1869) removed the Marnes à *Pholadomya ludensis* from the top of his Bartonian and Munier-Chalmas & Lapparent (1893) erected the Ludian Stage to include these plus the higher Gypse beds. Lapparent later (1906) retracted the Ludian. The legacy of this indecision and of the problems of correlation between the three basins of the type area has been fifteen different concepts of the Bartonian (Feuillée 1964). The large number of substages erected by authors (see Feuillée 1964: 40) in the Paris Basin have become restricted by general usage to two; the Auversian and Marinesian (see Pomerol 1980), the Ludian often being treated as an independent stage (especially by palaeomammalogists; see Cavelier 1980). All three have been widely used in correlating outside the Paris Basin despite the restricted nature of much of their aquatic invertebrate faunas.

The late Eocene Priabonian Stage (Munier-Chalmas & Lapparent 1893) was erected in Italy and has often been used since as a synonym of the Bartonian. Cavelier & Pomerol (1976) showed instead that the Priabonian was essentially equivalent to the Ludian and therefore succeeded the Bartonian, and was the terminal stage of the Eocene. The Eocene being now divisible into four main stages (Ypresian, Lutetian, Bartonian and Priabonian), problems arose as to where the Middle–Upper Eocene boundary should be drawn. The Bartonian was usually placed in the Upper Eocene when there were considered to be only three main stages, but Hardenbol & Berggren (1978) relegated it to the Middle as it was contemporaneous with planktonic foraminiferal zones normally placed in the Middle Eocene. These authors also preferred to define Palaeogene stages on planktonic foraminiferal zones because these were best for long range correlation. They equated the Bartonian with P13–14 (≡ NP16 upper–17).

Curry (1981) has argued that historically the cliffs near Barton, rather than localities in the Paris Basin as advocated by Morellet & Morellet (1934), should more correctly be considered stratotype of the Bartonian Stage. He proposed that the stratigraphical extent of the stage at the stratotype should correspond to the 'Barton Beds' as emended by Keeping (1887). The base could thus be defined biostratigraphically by the incoming of *Rhombodinium draco*, but the top only by the relatively local and uncorrelatable environmental change of marine to non-marine conditions.

The strata in England that Mayer-Eymar (1857) placed in his Bartonische Stufe were: 'white sands of Headon Hill, series of clayey and sandy beds of Alum Bay and clays of Barton' (translation). It is evident that his upper boundary was not in doubt here as he listed 'fresh-water formation of Hordwell and of Headon Hill, Alum Bay and Totland Bay' in the Ligurian Stage, beds which conformably overlie the Headon Hill Sands (herein Becton Sand Formation). His lower boundary, however, is in doubt in England for two reasons. Firstly, he indicated a gap with a '?' in the upper part of the underlying Parisian Stage (s.s. = Lutetian), above 'sands and marls of Bagshot ... and of Bracklesham'. Secondly, his 'clayey and sandy beds of Alum

Bay' are unidentifiable in detail but must include strata lower than just the Barton Clay at Alum Bay, since the Headon Hill Sands are already accounted for. His lower boundary in the Paris Basin was, however, not in doubt: it was between the 'marls and caillasses' (Upper Calcaire Grossier; Lutetian) and the 'sands of Beauchamp and Auvers' (Bartonian).

In erecting stages, Mayer-Eymar, like many other 19th Century workers, was essentially using fossils as worldwide time markers, but biostratigraphic successions were then too incomplete to give clear boundaries. Lithostratigraphic boundaries were thus relied upon for the stage (time) boundaries. Current French usage of the Bartonian substages Auversian and Marinesian (which together constitute Mayer-Eymar's concept of the English and northern French Bartonian after he had removed the Marls with *Pholadomya ludensis* in 1869) comprise sedimentary cycles which are not easy to correlate *per se* outside the local area. Hardenbol & Berggren's (1978) solution of using planktonic foraminiferal zones for defining the Bartonian allows ready use of a chronostratigraphic term over a wide area of the globe. However, this cannot be extended to the type area where the P zones are unknown, and their extrapolated positions using the intermediaries of dinocysts and sparse calcareous nannoplankton occurrences are likely to be inaccurate, although the NP16/17 boundary has recently been shown to occur between Barton beds B and E (Aubry 1983). On the basis of the name, it is accepted that the type locality of the Bartonian Stage should be the area of Barton. However, to follow Mayer-Eymar's type boundaries, it is necessary to consider the Paris Basin succession. If one accepts the Calcaire Grossier/Sables Moyens junction as the lower boundary and the removal of the Marls with *Pholadomya ludensis* from the top by Mayer-Eymar (1869), their correlatives in the Hampshire Basin would be the base of the oldest Barton Clay (as emended herein) for the lower boundary and the top of Barton bed I of the Becton Sand Formation for the upper boundary (see pp. 204–205).

These are the limits of the Bartonian followed herein (Auversian–Marinesian). With these boundaries, biostratigraphic correlation outside the north-west European basins would still be a problem, but which magnetostratigraphy (see Aubry 1983: fig. 35) and possibly the recognition of worldwide discontinuities reflecting sea level changes (see Vail & Hardenbol 1979) may eventually resolve.

Curry's (1981) recent restriction of Bartonian at the stratotype may turn out to be more useful biostratigraphically, since the incoming of *Rhombodinium draco* in the Anglo-Paris Basin area may approximate the base of P13. The evidence for this is the recognition in the Kallo borehole (Belgium) of basal NP16 near the base of the Argile d'Asse (Martini 1971) and a dinocyst assemblage *c.* 20 m higher in the same formation, suggesting to Châteauneuf (1980: 292) correlation with the upper Auversian of the Paris Basin and 'Lower Barton Beds' of Hampshire. This is further supported by Aubry's (1983) study of calcareous nannoplankton in the Hampshire and Paris Basins. In such a case much of the Auversian would have to be relegated to the Lutetian.

The lower limit of the Auversian in England. The lower limit of the Auversian in the Paris Basin corresponds with the base of the Formation de Mont St Martin. The strata in England which were long correlated with the whole of the Sables Moyens (Auversian) are the *Nummulites variolarius*-bearing 'Upper Bracklesham Beds' (= Selsey division of Curry *et al.*, 1977), e.g. by Wrigley on molluscs and Chandler on plants. The correlation was based on common occurrence in both strata of the foraminiferid *Nummulites variolarius*. It was not until Curry (1962) discovered *N. variolarius* in the Paris Basin Lutetian that this correlation was seriously questioned. Curry later (1967) equated only the upper part of the *N. variolarius*-bearing 'Upper Bracklesham Beds' (= upper Selsey division of Curry *et al.* 1977) with the Auversian, on the basis of the best statistical comparison of the mollusc faunas. Curry *et al.* (1978: 43) took a compromise position between the more extreme views of Pomerol (1961, 1964) on the one hand and of Morellet & Morellet (1948) and Curry (1967) on the other, and equated the Huntingbridge division (the topmost) of the Bracklesham Beds (= Elmore Member of the Barton Clay Formation herein), with the Auversian. *N. variolarius* does not occur in England above the Selsey division but this nummulite has now generally been abandoned as a means of

correlating the Auversian, because of its extended range outside this substage and its geographically restricted Bartonian occurrence.

The solution of Curry *et al.* (1978) is supported by ostracod faunas (see Keen 1978: 438–439) and is followed here. Thus base Elmore Member of the Barton Clay Formation ≡ base Auversian.

The upper limit of the Marinesian in England. The Barton Clay with its rich molluscan fauna has usually been correlated with the Sables de Cresnes and adjacent beds in the Paris Basin and therefore considered Marinesian (e.g. Morellet & Morellet 1948). Curry (1967), on the basis of the molluscs, placed only the 'lower Barton Beds' in the Marinesian. Other views have placed the 'Barton Beds' as low as the Auversian (Pomerol 1973) or as high as the Ludian (Pomerol 1964). The occurrence of species typical of the standard Calcareous Nannoplankton Zone NP17 in bed H (the upper part of which is defined here as the base of the Becton Sand Formation) aids correlation with more distant parts of the world but not with the Paris Basin (Martini 1971).

The Marnes à *Pholadomya ludensis* (type basal Ludian) represent a widespread but short-lived marine transgression in the Paris Basin and have a restricted fauna consisting largely of either long-ranged or endemic forms. Strata in England correlated with them have ranged from Barton Clay (Wrigley & Davis 1937) to Brockenhurst Bed (basal Middle Headon Beds) (Krutsch & Lotsch 1964). Curry (1967: 457) noted the occurrence of the gastropod *Turritella elongata* in both the Marnes à *Pholadomya ludensis* and 'near the boundary of the Middle and Upper Barton Beds' [Bed G?], although his chart (fig. 5) indicates correlation with lower parts of the 'Barton Beds'. Keen (1978: 439) suggested general correlation of the 'Barton Beds' with the Marnes à *Pholadomya ludensis* on the basis of ostracods, but he was not able to use this group to subdivide the former strata.

Châteauneuf (1980: 290) correlated the Middle Headon Beds with the Marnes à Lucines (overlying the Marnes à *Pholadomya ludensis*) and beds C–F of the Barton Clay with the Sables de Cresnes, using dinocyst evidence combined from his own work in the Paris Basin with that of Bujak *et al.* (1980) in the Hampshire Basin. This M. Headon Beds ≡ Marnes à Lucines correlation is also supported by ostracods (Keen 1978: figs 2–3). Grambast (1964) correlated the Lower Headon Beds with higher parts of the Marnes à *Pholadomya ludensis* on the basis of charophytes.

As the transgression of the basal Marnes à *Pholadomya ludensis* is very widespread in the Paris Basin and yet also very short-lived, it was probably allocyclically generated. An equally short-lived transgression within the Barton Clay and Becton Sand Formations and occurring between Barton Clay bed F and the base of the Middle Headon Beds is that of bed J, which forms the lower part of the fifth sedimentary cycle described below. The top of the fourth cycle (top of bed I in Christchurch Bay) is therefore here somewhat tentatively taken as the top of the Marinesian in the central Hampshire Basin succession.

The Auversian–Marinesian Boundary in England. As mentioned above, Curry *et al.* (1978) correlated the lowest parts (cycles 1 and 2) of the Barton Clay Formation (as 'Huntingbridge Formation') with the Auversian and much of the rest of the Barton Clay Formation (as 'Barton Beds') with the Marinesian, thus indirectly indicating a boundary correlation although the details of this were probably not intended. Châteauneuf (1980: 289–290, 302; text-fig. 50) correlated the *Nummulites prestwichianus* bed of the Barton Clay with an horizon high in the Sables de Beauchamp (Auversian) on the basis of the first occurrence of the dinocyst *Rhombodinium draco* in both (base of *Heteraulacacysta porosa* Assemblage Zone of Bujak *et al.*, 1980; and of the *Rhombodinium intermedium* and *Areosphaeridium dictyoplokos* Zone of Châteauneuf, 1980). He also correlated Barton Clay beds C–F with the Sables de Cresnes on the basis of the *Rhombodinium porosum* assemblage. This means that in the Hampshire Basin the Auversian–Marinesian boundary should lie somewhere between beds A1 and C at Barton Cliff. The complex of Marinesian strata below the Sables de Cresnes in the Paris Basin (Sables d'Ezanville, Calcaire de Ducy, Sables de Mortefontaine, Calcaire de St Ouen) are almost devoid

of dinocysts, their nannoflora is species poor and their mollusc faunas are essentially non-marine and long-ranging. Thus correlation in this part of the sequence is very difficult.

Radiometric Dates. Two studies (Odin *et al.* 1978; Hardenbol & Berggren 1978) have provided significantly different time scales. The latter is based on igneous rocks worldwide, the former on sedimentary glauconites in the basins discussed herein. Many of the earlier problems of glauconite dating have been overcome by Odin *et al.* but some still remain (see Fitch *et al.* 1978). The top and bottom of the Bartonian are dated by Hardenbol & Berggren (1978) as 40 and 44 million years BP (Ma) and by Odin *et al.* (1978) as 37 and 40 Ma respectively. Odin *et al.* (1978) dated the *N. prestwichianus* bed of the Barton Clay as 39 Ma. Cavelier (1980) gave a date of 41 ± 2 Ma (K/Ar) on upper Marinesian illites of the Paris Basin. Odin & Curry (1981) repeated the date by Odin *et al.* (1978) for the *N. prestwichianus* bed and gave the base of the Sables d'Auvers and equivalents as between 40·5 and 42 Ma.

Mammal correlation in the Bartonian (*sensu* Mayer-Eymar and Pomerol)

Introduction. The three sites, Elmore, Hengistbury and Barton Cliff, are the only ones in the marine Hampshire Basin sequence of the Bartonian which have yielded mammals. The fourth site, Creechbarrow, which contains the bulk of the species described here, is isolated in the far west of the basin and is dated as Marinesian according to its mammal fauna. Mammaliferous localities frequently occur in marginal areas or in fissure fillings whose direct stratigraphical relationships with standard marine successions are obscure. Mammals tend to be rapidly evolving and consequently their stratigraphical ranges are short. They are thus potentially very useful for correlation, but their rarity, especially in marine sequences, and their tendency towards endemism naturally reduce this utility.

Mammals are often sufficiently abundant in non-marine sequences to allow correlation over large areas, even though the relationships with the nearest marine sequence may not be known in detail. In continental Europe, a particular type of biostratigraphy has developed for the purpose of mammal correlation. This consists of a sequence of faunas, each taking its name from an important locality (e.g. Montmartre or Robiac), which have more recently been referred to as 'niveaux repères' (reference horizons; see Franzen 1968: 160; Hartenberger 1969). Subsequently discovered mammal faunas can either be identified with an existing fauna or given a name of their own and slotted into the sequence. The system was pioneered by Thaler (1965, 1966, 1972) and is also discussed by Savage & Russell (1977). One drawback to the system is the frequent reliance on evolutionary grade to determine position in the sequence. This can lead to circularity. In some cases, however, it is virtually unavoidable; e.g. the rich faunas of the Egerkingen fissures in Switzerland are largely unknown in any stratified sequence, marine or non-marine, although there is widespread agreement on their approximate sequential position. Their exact positions, however, do pose problems as they may straddle the Lutetian–Bartonian boundary (see p. 425).

Thaler introduced this system of zonation in an attempt to counter the frequent arbitrary and poorly founded attributions of various mammal faunas to certain marine stages. The latter had previously received a modified usage corresponding in the non-marine provinces to major mammal changes not correlatable with the real marine stage boundaries.

Many localities, which authors often confidently place in sequence with respect to each other, contain only a few species or varieties with known evolutionary polarities (e.g. Lissieu and Le Guépelle; see Ginsburg *et al.* 1965, Sudre 1972, Hartenberger 1972). Moreover, there is little chance of any two mammal localities being exactly the same age, so to refer one to a zone named from another locality gives a false impression of precision in age relationships. The basis for age relationship in biostratigraphy is always identity of named taxa and it seems appropriate to use these for names of zones in the conventional way as used for other groups. Suggestions for the exact order of localities within this framework can be made if no further useful breakdown into subzones can be made.

Niveaux repéres are usually defined either by one or a few index fossils, or by their total

faunal list which includes long- as well as short-ranged taxa. Correlation is often made despite absence of the index fossil. The reference of a given locality to a particular concurrent range zone (see Hedberg 1976: 55–57) with a list of the index species on which reference is based would be a more precise method and is advocated here.

Bosma (1974: 99–104) adopted a conventional method of mammalian biostratigraphy by erecting named biozones based on ranges of mammalian taxa rather than on vague faunal assemblages. She also erected the stage name Headonian to incorporate a cogent assemblage of these zones as part of a system of land mammal ages which was extended later to cover the whole of the Tertiary (Fahlbusch 1976). The Headonian corresponds approximately to the Ludian, whilst the next stage below (the Rhenanian) includes not only most of the Bartonian but also the Lutetian and late Ypresian (see also comments by Savage & Russell, 1977).

In the course of this study, the fitting of the relevant mammal faunas directly into the standard Bartonian sequence, without the need for a separate continental chronostratigraphic sequence, seemed possible, although requiring a considerable amount of extrapolation using partial sequences often with little overlap of either lithology or biota. European mammal faunas referable to the Bartonian are few and scattered but several are now known in the Hampshire and Paris basins (Ginsburg *et al.* 1965, Hooker 1972, 1977*b*, Louis 1976). Important fissure fillings occur in southern Germany, Switzerland and France (Dehm 1970, Stehlin 1903, Depéret 1894, Hartenberger *et al.* 1974); and important stratified non-marine sequences in southern France (Garimond *et al.* 1975).

Creechbarrow. The Creechbarrow Limestone Formation (restricted to Creechbarrow) was originally dated as early/middle Eocene because it was thought to be stratified within the pipe-clay series of Dorset which was correlated with the 'Lower Bagshot Beds' (Hudleston 1902*a*, *b*, 1903). The known fossils were algal-coated non-marine gastropods which gave little guide to correlation. Keeping's (1910) discovery of land snails and a '*Palaeotherium*' tooth fragment led him to consider the Creechbarrow Limestone as a mainland outlier of the Bembridge Limestone, which is otherwise restricted to the Isle of Wight. Keeping invented a sequence of beds at Creechbarrow which resembled the same sequence below the Bembridge Limestone on the Isle of Wight (see Arkell 1947). Bloomfield (1911), who had excavated with Hudleston, pointed out that Keeping's section appeared to have been taken from Alum Bay and that there was not enough room for all the strata at Creechbarrow. He ended his letter relevantly: 'Even if the Creechbarrow Limestone fauna and the Bembridge may be identical, they are not necessarily upon the same horizon, and may have existed in Lower Bagshot times. Why not?'

In fact, Keeping's supposed *Palaeotherium* tooth is an indeterminate root? fragment (see Hooker 1977*b*) and in any case the genus *Palaeotherium* ranges from late Lutetian to late Ludian. It is not restricted to beds of Bembridge Limestone age. His '*Dictulumus*' (misprint for *Dichobunus*) tooth (Keeping 1912) is in fact *Lophiotherium*, a genus absent from the late Ludian. Hooker (1977*b*) recorded an extensive mammal fauna from Creechbarrow which was unlike that of the Bembridge Limestone. Preece (1980*a*) revised the molluscs and showed that some of the land snails (e.g. '*Filholia*' *elliptica*) had been misidentified and that only three Creechbarrow species were otherwise known in England only from the Bembridge Limestone. The non-mammal biota of the Creechbarrow Limestone is given below; the mammal list is at the beginning of the systematics section (Table 1, p. 212). Comparable biotic lists for the Bembridge Limestone can be found in Preece (1976, 1981) (terrestrial gastropods); Edwards (1852) (other molluscs, unrevised); Hooker & Insole (1980) (mammals).

This list is based on Hooker (1977*b*) and Preece (1980*a*, 1981). Dr R. Estes identified the Ophidia, Dr A. C. Milner identified the ?lacertilian and Dr P. D. Taylor revised the bryozoan names.

Whereas the typically longer-ranging gastropods have much in common between the Creechbarrow and Bembridge Limestone, the mammals are totally different at species level and moderately different at generic level.

Monera: Cyanophyta indet. (Pl. 35, figs 1–2)

Animalia: Bryozoa (derived from the Chalk)
Meliceritites sp.
'*Vincularia*' sp.
Woodipora sp.
vinculariiform ascophorans indet.

Mollusca*–Gastropoda
Proserpina cf. *woodwardi* Preece 1981
Cochlostoma heterostoma (Edwards 1852)
Viviparus angulosus (J. Sowerby 1817)
V. cf. *lentus* (Solander 1766)
Bembridgia cincta (Edwards 1852)
cf. *Coptostylus brevis* (J. de C. Sowerby 1826)
Lymnaea cf. *longiscata* (Brongniart 1810)
Palaeoxestina occlusa (Edwards 1852)
Milax cf. *latus* (Edwards 1852)
'*Clausilia*' sp.
Filholia laevolonga (Boubée 1831)
Palaeoglandina costellata (J. Sowerby 1822)
cf. *Archygromia durbani* (Edwards 1852)
Megalocochlea pseudoglobosa (d'Orbigny 1850)
cf. *Klikia vectiensis* (Edwards 1852)

Mollusca–Bivalvia
Unio brightoni Woodward 1965

?Arthropoda–?Insecta
?Trichoptera larval cases (Pl. 35, fig. 3)
?Chironomidae larval tubes (Pl. 35, fig. 1b)
indet. burrows (Pl. 35, fig. 4)

Pisces–Teleostei
Characoidei indet. (teeth) (Pl. 35, fig. 5)
?Siluriformes indet. (dermal bones)
indet. (palatal bones)

Reptilia–Crocodilia indet. (Pl. 35, fig. 6)

Reptilia–Chelonia indet.

Reptilia–Ophidia
cf. *Cadurceryx* sp.
indet.

Reptilia–?Lacertilia indet.

* References to authors of the molluscan species are to be found in Preece (1980*a*), Hooker (1977*b*) or herein.

Range of Bartonian mammalian taxa and definition of zones. A large number of the Bartonian mammal species have restricted ranges. This is partly geographical but also, more importantly for correlation, stratigraphical. Although many of the localities are not in sequences, the few that are, especially those in marine sequences, show that these ranges are often chronologically short. As an alternative to the 'niveaux-repères' system (p. 418), two mammalian concurrent range zones are erected here to span the late Lutetian and Bartonian. The mammalian zones which Bosma (1974) erected for the Headonian are taxon range zones and concurrent range zones. The concurrent range zones defined here are intended to cover the whole of the west European terrestrial area (with adjacent marine basins included) as it was in Eocene times (see below, p. 449). To achieve this they include a number of taxa, all of which occur together at at least one locality. Because of the general rarity of stratified mammal localities and the isolation of non-stratified ones, neither total ranges nor (in most cases) precise limits of the zones are known. Nevertheless, the taxa defining successive zones do not overlap even in the richest known faunas and their limits may eventually be found to approximate to time horizons.

i. The *Palaeotherium eocaenum–Lophiodon rhinocerodes* Concurrent Range Zone.

This is defined by the total known ranges of *Palaeotherium eocaenum*, *Lophiodon rhinocerodes*, *Lophiotherium pygmaeum*, *Dichobune robertiana*, *Cebochoerus ruetimeyeri*, *Haplobunodon solodurense* and *Pseudamphimeryx schlosseri*.

Various other species whose ranges begin earlier also end at the top of the zone; e.g. *Lophiodon cuvieri*, *L. parisiense*, *Plesiarctomys spectabilis* and *Ailuravus picteti*. See Table 36 for the distribution of the taxa defining the zone. Egerkingen γ and α are the only localities where all the taxa defining the zone occur. The zone ranges from the Upper Calcaire Grossier to the Sables Moyens in the stratified sequence of the Paris Basin.

ii. The *Lophiodon lautricense–Lophiotherium siderolithicum* Concurrent Range Zone.

This is defined by the total known ranges of *Lophiodon lautricense*, *Lophiotherium siderolithicum*, *Palaeotherium lautricense*, *Leptolophus stehlini*, *Acotherulum campichii*, *Haplobunodon venatorum*, *Plesiarctomys hurzeleri*, *Ailuravus stehlinschaubi*, *Xiphodon castrense* and *Simamphicyon helveticus*.

Cebochoerus robiacensis and *Pseudoloris crusafonti* are also restricted to the zone but are not sufficiently widespread to be included. *Lophiodon thomasi* may also be restricted to the zone but

Table 36 Distribution of the taxa defining the Zone of *Palaeotherium eocaenum–Lophiodon rhinocerodes*. Sources: Brunet & Gabilly (1981); Depéret (1906); Franzen (1968); Ginsburg *et al.* (1965, 1977); Louis (1976); Stehlin (1903, 1904*b*, 1905*a*, *b*, 1906, 1908, 1910*a*, 1910*b*); Sudre (1972, 1978*b*); and Wood (1976*a*).

	Pseudamphimeryx schlosseri	*Haplobunodon solodurense*	*Cebochoerus ruetimeyeri*	*Dichobune robertiana*	*Lophiotherium pygmaeum*	*Lophiodon rhinocerodes*	*Palaeotherium eocaenum*
Grès de Brenne, Fonliasmes						×	
Upper Calcaire Grossier, Paris Basin			×	×		×	×
Sables d'Auvers, Le Guépelle							×
'Sidérolithique', Egerkingen γ and Huppersand	×	×	×	×	×	×	×
'Sidérolithique', Egerkingen α	×	×	×	×	×	×	×
'Sidérolithique', Egerkingen β	×	×	×	×	×		×
'Sidérolithique', Lissieu	×			×	×	×	
Calcaire de Castres, Roc de Lunel						×	

Table 37 Distribution of the taxa defining the Zone of *Lophiodon lautricense–Lophiotherium siderolithicum*. Sources additional to those of Table 36: Depéret (1910); Hooker (1977*a*, *b*); Hooker & Insole (1980); Maack (1865); Remy (1965); Stehlin (1918); Sudre (1971); and Wood (1970). Other records are based on information herein and the author's personal observations in museum collections.

	Xiphodon castrense	*Haplobunodon venatorum*	*Acotheridium campichii*	*Palaeotherium lautricense*	*Leptolophus stehlini*	*Simamphicyon helveticus*	*Ailuravus stehlinschaubi*	*Plesiarctomys hurzeleri*	*Lophiotherium siderolithicum*	*Lophiodon lautricense*
Creechbarrow Limestone, Creechbarrow		×	×				×	×	×	
Barton Clay, Hengistbury										cf.
Calcaire de St Ouen, Paris and Grisolles			×							cf.
Sables de Cresnes, Berville										×
'Sidérolithique', Eclépens-Gare	×	aff.	×	×	(×)	×	×	(×)	×	×
Lower Calcaire de Fons, Robiac	×		×		×	×		×	×	×
Sables du Castrais, Le Castrais	×			×	×			×		×
'Sidérolithique', Le Bretou	×					×				
'Sidérolithique', Heidenheim										×

the uniqueness of its occurrence and problems over its exact stratigraphical position require its exclusion. *Anchilophus desmarestii* was considered by Sudre (1969*a*) to be a characteristic Marinesian species, but it also occurs, admittedly with a cf. determination, at Egerkingen where it overlaps with the *eocaenum–rhinocerodes* Zone taxa. A number of fragmentary specimens of a large *Lophiodon* species, usually referred to *L.* cf. *lautricense*, occur at more than one level in marginal calcareous facies cited as being lateral equivalents of the Sables Moyens. They are from Arcis-le-Ponsart (Louis 1976) and Nogent-l'Artaud (Morellet & Morellet 1948), and their horizons have been correlated with the Facies ('Horizon') du Guépelle (Morellet & Morellet 1948) which contains an *eocaenum–rhinocerodes* Zone fauna. The specimens have never been figured or described in detail. Some overlap of the zones may occur, or the records may not represent *L. lautricense* but a different species, or the lithostratigraphic correlation of these marginal facies may not be accurate. A potential immediate ancestor for *L. lautricense* is not known. *L. rhinocerodes* has been discarded from this role by Sudre (1971) and his alternative (*L. cuvieri*) is considered herein (p. 375) to be more closely related and probably ancestral to *L. thomasi*. See Table 37 for distribution of taxa defining the zone.

Eclépens-Gare is the only locality where all the taxa defining the zone occur together. The zone ranges from the Calcaire de St Ouen to the Sables de Cresnes in the stratified sequence of the Paris Basin. The faunal change immediately above this zone is well documented in a stratified non-marine sequence in the Alès Basin, southern France (Garimond *et al.* 1975). There may be a gap between the *lautricense–siderolithicum* Zone and that of *Thalerimys* [*Isoptychus*] *headonensis* (Bosma 1974) Vianey-Liaud 1979, defining the base of the Headonian in southern England. There is room in the earlier Ludian for the faunas of Fons (U. Calcaire de Fons) (Garimond *et al.* 1975).

The *lautricense–siderolithicum* Zone seems to mark a particularly distinctive phase in European Eocene mammal faunas. Of the total of over 100 named and unnamed species-group mammal taxa occurring in this Zone, only 3 range above and below; 14 range only below; 33 range only above; whilst 53 are unknown outside the zone. Of the 53 restricted forms, 8 have likely ancestors in the zone below; 13 have likely descendants in strata immediately above; whilst 2 are sandwiched between respective ancestors and descendants (see Table 38).

Table 38 *L. lautricense–L. siderolithicum* Zone species-group taxa and main localities. The range column indicates occurrence extending below ◐, above ◑, above and below ●, or restricted to the zone ○. ?, aff., or cf. applied to one side or other of the symbol refers to qualification of the earlier or later record(s). Note that *Amphiperatherium ?lamandini* may be the same as *A.* aff. *goethei*, and that Berville, Heidenheim and Hengistbury (not listed) only contain *Lophiodon lautricense* (or cf.). Brackets indicate doubtful provenance. Sources as for Tables 36–37 with addition of Crochet *et al.* (1981).

	Range	Creechbarrow	Barton C–F	Grisolles	Paris	Sergy	Eclépens-Gare	Le Castrais	La Guittardie	Robiac	Le Bretou
Amphiperatherium giselense	●	–	–	×	–	–	–	–	–	–	–
A. minutum	◑	–	–	×	–	–	–	–	–	–	×
A. bourdellense	●	–	–	×	–	–	–	–	–	–	×
A. goethei	◐	aff.	–	–	–	–	–	–	–	–	–
A. lamandini	◑	–	–	×	–	–	–	–	–	–	–
A. fontense	◑	×	–	–	–	–	–	–	–	×	×
Peratherium sudrei	◐	–	–	×	–	–	–	–	–	×	–
P. bretouense	○	–	–	–	–	–	–	–	–	–	×
P. lavergnense	◑	–	–	–	–	–	–	–	–	–	×
Saturninia mamertensis	?◐	–	–	–	–	–	–	–	–	×	×

Table 38 (*continued*)

	Range	Creechbarrow	Barton C–F	Grisolles	Paris	Sergy	Eclépens-Gare	Le Castrais	La Guittardie	Robiac	Le Bretou
S. grisollensis	○	–	–	×	–	–	–	–	–	?	–
S. hartenbergeri	◐	–	–	–	–	–	–	–	–	×	–
S. beata	◑	–	–	–	–	–	–	–	–	–	×
S. grandis	○	–	–	×	–	–	–	–	–	?	–
S. intermedia	?◐	–	–	×	–	–	–	–	–	–	–
Gesneropithex grisollensis	◑aff.	–	–	×	–	–	–	–	–	–	–
G. figularis	○	×	–	–	–	–	–	–	–	–	–
G. sp. (Robiac)	○	–	–	–	–	–	–	–	–	×	–
Rhinolophus sp. 1	○	–	–	–	–	–	–	–	–	–	×
Vespertiliavus gracilis	◑	–	–	–	–	–	–	–	–	–	cf.
V. wingei	◑	–	–	–	–	–	–	–	–	–	×
V. sp. 1	◑	–	–	–	–	–	–	–	–	–	×
Nannopithex quaylei	○	×	–	–	–	–	–	–	–	–	–
N. sp. 1	○	×	–	–	–	–	–	–	–	–	–
Pseudoloris crusafonti	○	cf.	–	×	–	–	–	–	–	–	–
P. parvulus	◑	–	–	–	–	–	–	–	–	–	×
Necrolemur zitteli	◑	–	–	×	–	–	–	–	–	×	×
Microchoerus sp. (Grisolles)	○	–	–	×	–	–	–	–	–	–	–
M. wardi	○	×	–	–	–	–	–	–	–	–	–
M. creechbarrowensis	○	×	–	–	–	–	–	–	–	–	–
Europolemur collinsonae	○	×	–	–	–	–	–	–	–	–	–
Leptadapis magnus	◑?	aff.	–	–	–	–	–	–	–	–	–
Adapis sudrei	○	–	–	cf.	–	–	–	–	–	×	–
?A. laharpei	○	–	–	–	–	–	×	–	–	–	–
Plesiarctomys curranti	○	×	–	–	–	–	(cf.)	–	–	–	–
P. hurzeleri	○	×	–	–	–	–	(×)	×	–	×	–
Ailuravus stehlinschaubi	○	×	–	–	–	–	×	–	–	–	–
Gliravus robiacensis	◑aff.	–	–	aff.	–	–	–	–	–	×	×
Sciuroides rissonei	○	×	–	–	–	–	–	–	–	–	–
S. russelli	○	–	–	×	–	–	–	–	–	–	–
S. siderolithicus	○	–	–	–	–	–	×	–	–	×	×
Treposciurus helveticus preecei	○	×	–	–	–	–	–	–	–	–	–
Suevosciurus authodon	○	×	–	–	–	–	–	–	–	–	–
Paradelomys crusafonti	◑	–	–	cf.	–	–	–	–	–	cf.	cf.
Elfomys tobieni	◑	–	–	–	–	–	–	–	–	×	–
Pseudoltinomys mamertensis	◑	–	–	?	–	–	–	–	–	–	aff.
Theridomys varleti	○	–	–	×	–	–	–	–	–	–	–
Remys minimus	○	–	–	–	–	–	–	–	–	×	cf.
Heterohyus sudrei	◑	cf.	–	×	–	–	–	–	–	×	–
H. nanus	◑	aff.	–	–	–	–	–	–	–	×	–
H. morinionensis	○	×	–	–	–	–	–	–	–	–	–
Cynohyaenodon cayluxi	○	–	–	–	–	–	–	–	–	–	×
Hyaenodon heberti	◑	–	–	–	–	–	–	–	–	aff.	–
Simamphicyon helveticus	○	–	–	–	–	–	×	–	–	×	×
Quercygale angustidens	◑	–	–	–	–	–	×	–	–	×	×
Vulpavoides cooperi	○	×	–	–	–	–	–	–	–	–	–
Propalaeotherium parvulum	◐	aff.	–	–	–	–	aff.	–	–	–	cf.
Lophiotherium siderolithicum	○	×	–	–	–	–	×	–	–	×	–
Anchilophus desmarestii	cf.◐	–	–	–	×	–	(×)	–	–	cf.	×
A. gaudini	◑cf.	–	–	–	–	–	×	cf.	–	cf.	×
A. dumasii	◑	–	–	–	–	–	×	–	–	cf.	cf.

Table 38 (*continued*)

	Range	Creechbarrow	Barton C–F	Grisolles	Paris	Sergy	Eclépens-Gare	Le Castrais	La Guittardie	Robiac	Le Bretou
A. depereti	◐	–	–	–	–	–	–	cf.	–	cf?	–
Plagiolophus curtisi curtisi	○	–	×	–	–	–	–	–	–	–	–
P. curtisi creechensis	○	×	–	–	–	–	–	–	–	–	–
P. cartailhaci	○	–	–	–	–	–	–	×	–	×	–
P. annectens	◑	–	–	–	–	–	aff.	aff.	–	aff.	aff.
Leptolophus nouleti	○	–	–	–	–	–	–	×	–	–	–
L. stehlini	○	–	–	–	–	–	(×)	×	–	×	–
Palaeotherium ruetimeyeri	◐	–	–	–	–	–	–	–	–	aff.	–
P. pomeli	○	–	–	–	–	–	–	×	×	×	–
P. castrense castrense	◐	–	–	–	–	–	–	×	–	–	–
P. c. robiacense	○	–	–	–	×	–	–	–	×	×	–
P. siderolithicum	◑	–	–	–	–	–	×	×	–	×	cf.
P. lautricense	○	–	–	–	–	–	cf.	×	–	–	–
P. muehlbergi	◑	–	?aff.	–	–	–	–	–	–	–	–
Lophiodon lautricense	○	–	–	–	cf.	–	×	×	–	×	–
L. thomasi	○	–	–	–	–	×	–	–	–	–	–
L. tapiroides	◐	–	–	–	–	–	×	–	–	–	–
Chasmotherium cartieri	◐	–	–	–	–	–	×	–	–	×	–
Cebochoerus minor	◑	–	×	–	–	–	×	×	–	–	?
C. robiacensis	○	×	–	–	–	–	–	×	–	×	–
Acotherulum campichii	○	×	–	×	–	–	×	–	–	×	–
Mixtotherium gresslyi	●	aff.	aff.	–	–	–	–	aff.	–	–	–	–
M. infans	◐	–	–	–	–	–	cf.	–	–	–	–
Haplobunodon venatorum	○	×	–	–	–	–	aff.	–	–	–	–
Anthracobunodon louisi	○	–	–	×	–	–	–	–	–	–	–
Choeropotamus lautricensis	○	–	–	–	–	–	–	×	–	×	–
Dacrytherium elegans	◑	×	–	–	–	–	×	–	–	–	aff.
Catodontherium robiacense	○	–	–	–	–	–	×	–	–	×	–
C. ?paquieri	○	–	–	–	–	–	–	×	–	–	–
Leptotheridium lugeoni	◑	–	–	–	–	–	×	–	–	–	–
L. traguloides	◐	–	–	–	–	–	–	–	–	cf.	aff.
Tapirulus schlosseri	◑	?	–	–	–	–	×	–	–	×	×
Robiacina minuta	○	–	–	–	–	–	–	–	–	×	×
R. weidmanni	○	–	–	–	–	–	×	–	–	–	–
Xiphodon castrense	○	–	–	–	–	–	×	×	–	×	×
Paraxiphodon cournovense	○	–	–	–	–	–	–	–	–	×	–
Haplomeryx picteti	○	–	–	–	–	–	×	–	–	×	×
Dichodon cervinus	◑	cf.	–	–	–	–	cf?	–	–	–	–
D. subtilis	○	–	–	–	–	–	×	–	–	–	–
Pseudamphimeryx pavloviae	◑	–	–	–	–	–	–	–	–	×	×
P. renevieri	◑	–	–	–	–	–	×	–	–	aff.	–
P. valdensis	○	–	–	–	–	–	×	–	–	–	–

iii. Discussion. An attempt has been made in each zone to find the same genera represented by different species, and use them as zonal indices, with varying degrees of success. In some cases it is thought that the species represent stages in evolutionary sequences – e.g. *Lophiotherium pygmaeum* to *L. siderolithicum* (see Savage *et al.* 1965, and herein); *Palaeotherium eocaenum* to *P. lautricense* (see Franzen 1968); and *Haplobunodon solodurense* to *H. venatorum* (p. 409). In the former case, transitional 'advanced' forms of *L. pygmaeum* occur at Egerkingen *β* (see

Stehlin 1905*b*). In the case of *Ailuravus stehlinschaubi* and *Lophiodon thomasi* the probable ancestral species (*A. picteti* and *L. cuvieri*) occur in the *eocaenum–rhinocerodes* Zone, but also range down into earlier Lutetian strata. Three of the *lautricense–siderolithicum* Zone index species (*L. siderolithicum*, *Acotherulum campichii* and *Plesiarctomys hurzeleri*) also have probable descendant species (*L. cervulum*, *A. saturninum* and *P. gervaisii*) in Ludian strata. In the former case, the Alès Basin has yielded a series of transitional forms from the Fons localities, linking *L. siderolithicum* from Robiac to *L. cervulum* from Euzet (Remy 1967, Garimond *et al.* 1975). The species *Lophiodon lautricense*, *Chasmotherium cartieri*, *Leptolophus stehlini* and *Ailuravus stehlinschaubi* last occur at the top of the *lautricense–siderolithicum* Zone, marking also the last appearance of the family Lophiodontidae, the family Helaletidae in Europe, the genus *Leptolophus* and the subfamily Ailuravinae in the stratigraphic record.

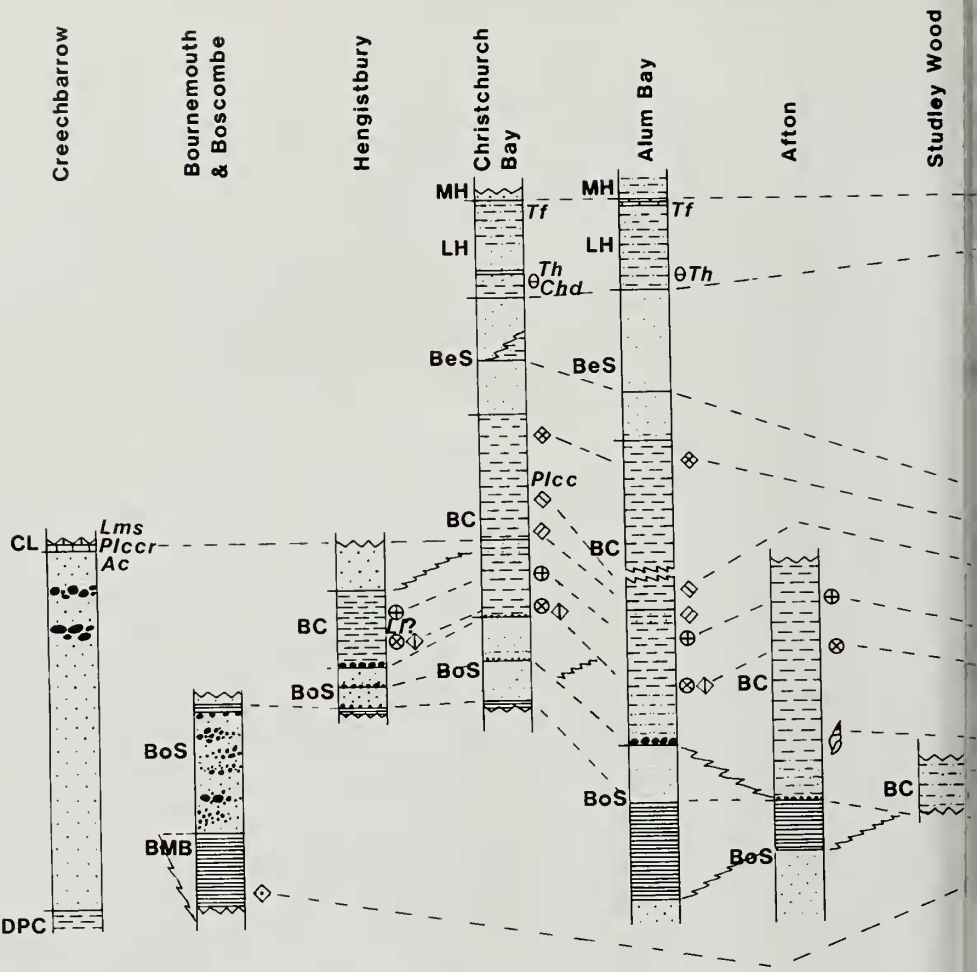
The principal and most widespread taxa as well as those forming stratigraphical morphoclines have been chosen to define the two zones erected here. Numerous other lesser-known taxa with assumed similar evolutionary relationships occur through this period of time.

iv. Further subdivision by mammalian biostratigraphy. It is difficult to locate the Lutetian–Auversian boundary within the *eocaenum–rhinocerodes* Zone. Changes from one fauna to another in the Egerkingen fissures are highly relevant to this problem but the stratigraphical order of these fissures is unknown, being postulated on evolutionary grade. It is probable that Egerkingen β is the most recent; Egerkingen α appears more advanced than Egerkingen γ but less so than Egerkingen β (see Hartenberger 1972). It is possible that with the probable chronological range involved these fissures straddle the Lutetian–Auversian boundary. A study in progress on early species of *Plagiolophus* may cast further light on this problem.

Detailed correlation between the Hampshire and Paris basins has already been shown to be a problem and has ramifications in any attempt to arrange the various Bartonian mammal localities in succession. Text-fig. 67, however, attempts this by piecing together the various partial correlations which have been made using different groups of organisms.

Hartenberger & Louis (1976) placed the mammal fauna of Grisolles, which occurred in about the middle of the Calcaire de St Ouen in the east of the Paris Basin, later than Robiac and earlier than Fons 4 in the scale of niveaux-repères, all three being included in the Marinesian. This contrasts with most authors who place Fons 4 near the base of the Ludian (e.g. Garimond *et al.* 1975) and is contrary to evidence from the charophytes (Grambast 1962, 1964, 1972), which correlates Robiac with higher, not lower, parts of the Calcaire de St Ouen. Moreover, Grisolles contains a number of species typical of the *lautricense–siderolithicum* Zone but which do not occur in strata immediately overlying those from which the Robiac fauna has been obtained (Garimond *et al.* 1975): i.e. *Pseudoloris crusafonti*, *Adapis* cf. *sudrei* and *Acotherulum campichii*. The rest of the fauna too is very different from those of Fons 1, 2, 5, 6 and 7, and also from Le Bretou (except for some long-ranging species), which occupy Hartenberger & Louis' (1976) postulated level for Grisolles in the Alès Basin (see Sigé 1976, Sudre 1978*b*, Louis & Sudre 1975, Crochet 1979, 1980 and Crochet *et al.* 1981 for faunal details). Grisolles, which is demonstrably well within the Bartonian, is therefore considered to be earlier than Robiac which is dated as late Marinesian because of its position immediately below the *L. lautricense–L. stehlini* extinction datum.

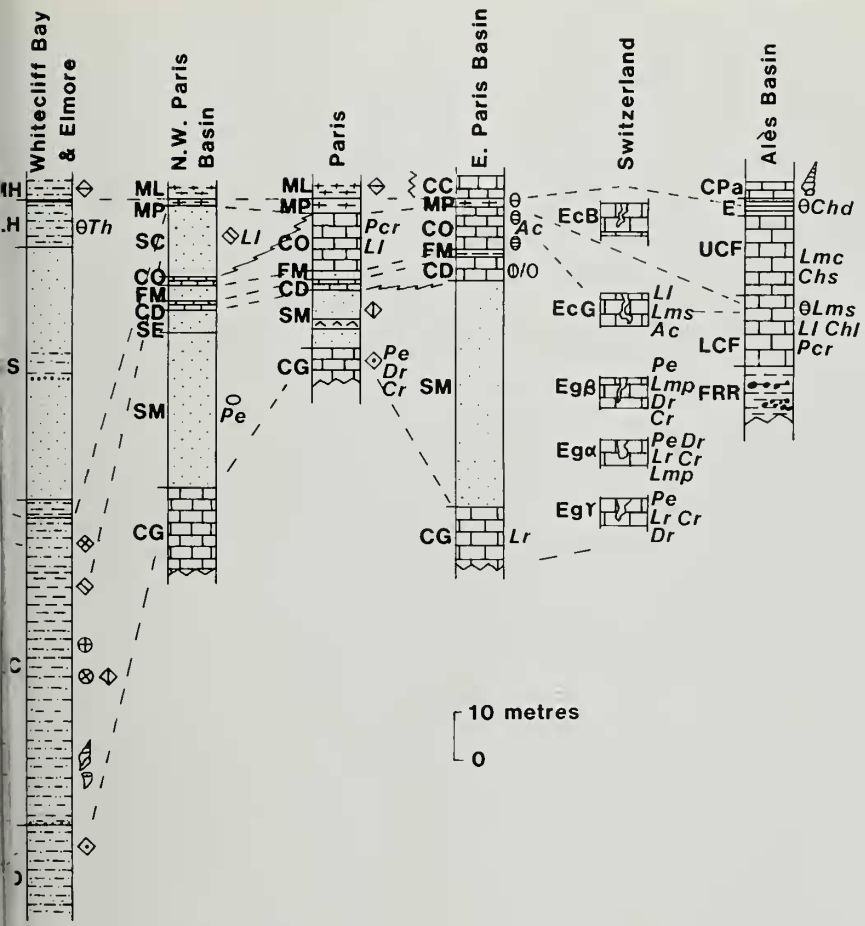
The reasons given by Hartenberger & Louis (1976) for their dating of Grisolles relative to strata in the Alès Basin was based on evolutionary grade in certain rodents. The arguments ran thus: 1, *Theridomys varleti* and *Pseudoltinomys* sp. are more primitive than *T. euzetensis* and *P. mamertensis* from Fons 4; 2, the *Pseudoltinomys* is very similar to that from Le Bretou, a fissure locality considered slightly younger than Robiac; and 3, *Suevosciurus russelli* and *Gliravus* aff. *robiacensis* are more advanced than *S. romani* and *Gliravus robiacensis* from Robiac. The *Pseudoltinomys* by their own admission is very poorly known; the intrageneric relationships of *Suevosciurus russelli* (shown on p. 300 to belong to *Sciuroides*) with *S. romani* (synonymized with *Sciuroides siderolithicus*, p. 300) are obscure; it seems likely that *S. siderolithicus* gave rise to *S. ehrensteinensis* via transitional forms recorded at Weidenstetten (Schmidt-Kittler 1971*a*) and Eclépens B, whereas *S. russelli* is closer to *S. rissonei*, which occurs at Creechbarrow



Text-figure 67 Correlation of European Bartonian strata. Stratigraphical columns range into strata higher and lower than Bartonian in most cases. For key to lithological symbols, see Text-fig. 2, p. 201. Abbreviations of lithostratigraphy are given on left of columns and abbreviations (mammals) and symbols (other biota) of biostratigraphy are given on right of columns. Jagged break in Alum Bay column indicates the omission of *c.* 9m of Barton Clay.

Abbreviations of lithostratigraphy: BC = Barton Clay Formation; BeS = Becton Sand Formation; BMB = Bournemouth Marine Beds; BoS = Boscombe Sands; CC = Calcaire de Champigny; CD = Calcaire de Ducy; CG = Calcaire Grossier; CL = Creechbarrow Limestone Formation; CO = Calcaire de St Ouen; CPa = Calcaire à *Potamides aporoschema*; DPC = Dorset pipe clays; E = marnes d'Euzet; EcB = Eclépens B; EcG = Eclépens-Gare; Eg = Egerkingen; FM = Formation de Mortefontaine; FRR = formation rouge de Robiac; LCF = lower Calcaire de Fons; LH = Lower Headon Beds; MH = Middle Headon Beds; ML = Marnes à *Lucina inornata*; MP = Marnes à *Pholadomya ludensis*; SC = Sables de Cresnes; SD = Selsey division; SE = Sables d'Ezanville; SM = Sables Moyens; UCF = upper Calcaire de Fons.

associated with a typical *lautricense–siderolithicum* Zone fauna. This leaves only the *Gliravus* at Grisolles supporting a younger age than Robiac. The coefficients of variation given by Hartenberger & Louis (1976: 89, tab. 4) for the lengths of upper and lower preultimate molars of *Gliravus* aff. *robiacensis* from Grisolles exceed 9, which is a good indication that more than one species is represented. In view of these problems, it is considered that more confidence can be



Text-figure 67, continued. Abbreviations of mammal taxa: *Ac* = *Acotherulum campichii*; *Cr* = *Cebochoerus ruetimeyeri*; *Chd* = *Choeropotamus depereti*; *Chl* = *C. lautricensis*; *Chs* = *C. sudrei*; *Dr* = *Dichobune robertiana*; *Ll* = *Lophiodon lautricense*; *Lr* = *L. rhinocerodes*; *Lmc* = *Lophiotherium cervulum*; *Lmp* = *L. pygmaeum*; *Lms* = *L. siderolithicum*; *Pcr* = *Palaeotherium castrense robiacense*; *Pe* = *P. eocaenum*; *Plcc* = *Plagiolophus curtisi curtisi*; *Plccr* = *P. curtisi creechensis*; *Tf* = *Thalerimys fordi*; *Th* = *T. headonensis*.

Biotic symbols: Dinocysts: ◇ = first occurrence of *Areoligera undulata* and *Areosphaeridium multicornutum*; ◈ = first occurrence of *Rhombodinium draco*; ◈ = base zone BAR-2 of Bujak *et al.* (1980); ◇ = first occurrence of *R. porosum*; ⊗ = base zone BAR-4; ⊖ = first occurrence of *Homotryblium floripes* and *Kisselovia clathrata angulosa*. Charophytes: ○ = zone of Nogent-l'Artaud; ◍ = zone of Chéry-Chartreuve; ⊖ = zone of St Ouen; ⊖ = zone of Robiac; ⊖ = zone of Verzenay (base). *Nummulites*: ⊗ = *N. prestwichianus*; ⊕ = *N. rectus* first appearance. Coral: ▽ = *Paracyathus*. Gastropods: 𝒻 = *Ectinochilus planum*; 𝒻 = *Potamides aporoschema*. Ostracod: ○ = *Cytheretta cellulosa*.

Sources: Bosma (1974), Bujak *et al.* (1980), Châteauneuf (1980), Costa *et al.* (1976), Curry (1942, 1977), Depéret (1910), Ginsburg *et al.* (1965, 1977), Grambast (1962, 1964, 1972), Keen (1978), Kemp *et al.* (1979), Lemoine & Abrard (1926), Louis & Sudre (1975), Roman (1904), Stehlin (1903, 1904*b*, 1905*b*, 1906, 1908, 1918), Sudre (1969*a*, 1978*b*).

attached to other elements in the mammal fauna and to the charophytes than to rather generalized ideas of evolutionary grade in those rodent species whose exact relationships are still unclear.

Mammals recorded from other Calcaire de St Ouen localities include *Palaeotherium castrense robiacense* Franzen 1968 from about the middle of the formation in Paris (Lemoine & Abrard 1926). This subspecies is recorded from the top of the *lautricense–siderolithicum* Zone at Robiac,

associated with the Robiac charophyte zone. Fossils characterizing the latter zone are recorded from immediately below the Marnes à *Pholadomya ludensis* in the northern Paris Basin, thought to be equivalent to the Sables de Monceau in the region of Paris (Cavelier 1979: 157). *P. c. robiacense* appears thus to occur at a lower horizon here, but the problems posed for correlation within the Paris Basin by the condensed sequences and the lateral facies changes near the basin margins make this by no means the only interpretation. The relationship to Grisolles, also occurring at about the middle of the formation, is equally a problem, especially as there is no mammalian faunal overlap between the two localities.

In England, only two taxa are common to the Creechbarrow Limestone and the Barton Clay: Microchiroptera gen. et sp. indet. 1 (p. 241) and *Plagiolophus curtisi* (p. 353). The slight differences of size and morphology between the two assemblages of the latter have resulted in two subspecies being described. On the theoretical concept of evolutionary grade, *P. curtisi creechensis* from Creechbarrow is considered slightly more primitive than *P. curtisi curtisi* from Barton bed D/E, and therefore slightly earlier. Creechbarrow and Grisolles share only two short-ranged species: *Pseudoloris crusafonti* (cf. determination at Creechbarrow) and *Acotherulum campichii*. Ideas of evolutionary grade in two other genera give contradictory results: Creechbarrow *Sciuroides rissonei* appears in some respects to be more primitive than Grisolles *S. russelli*, whereas the Grisolles *Microchoerus* is more primitive than and intermediate in size between Creechbarrow *M. wardi* and *M. creechbarrowensis*. The choice is difficult but the evidence from *Microchoerus* is more convincing as it fits better with the subsequent sequence of events in *Microchoerus* evolution; in contrast, the relationships of *S. russelli* are more obscure. Grisolles is thus tentatively considered to be slightly earlier than Creechbarrow, which in this case must be Marinesian rather than late Auversian.

The various mammaliferous localities of the Castrais region of the Aquitaine Basin (Sables du Castrais) are thought to vary somewhat in age (see Richard 1946 for faunal lists; Sudre 1969*a*). They were considered by Remy (1965) to be earlier than Robiac because they contained a lower-crowned and therefore more primitive species of *Leptolophus*, *L. nouleti* (Stehlin 1904*a*) Remy 1965, than at Robiac (*L. stehlini*). Increase in crown height is almost universally considered to be an advancement, but at other localities in Le Castrais *L. stehlini* also occurs. It is most likely that the latter are younger than the localities yielding *L. nouleti*. Castrais *L. stehlini*, moreover, has slightly lower crown height than Robiac *L. stehlini*, although the difference is not nearly so marked as with *L. nouleti*. *L. stehlini* from Mormont (Eclépens A and probably, although not labelled, Eclépens-Gare) is very similar in crown height to that of Le Castrais, suggesting close correlation. An $M_{1/2}$ from the Auversian of Le Guépelle was recorded as '*Plagiolophus* taille de *P. annectens*' by Ginsburg *et al.* (1965). It more closely resembles *Leptolophus* in morphology and is at least as low-crowned as *L. nouleti*. It is thus possible that the Castrais localities with *L. nouleti* are as old as Auversian.

Other elements in the Castrais and Eclépens-Gare faunas have been shown to be slightly different from those of Robiac, indicating that they are probably slightly older (e.g. Sudre 1969*a*; Franzen 1968), but relationships with localities such as Creechbarrow and Grisolles are less easy to envisage. Creechbarrow and Eclépens-Gare share a number of short-ranged species (viz. *Lophiotherium siderolithicum*, *Haplobunodon venatorum* and *Ailuravus stehlinschaubi*), but there are subtle differences in these, e.g. in size, which could just as easily result from geographical as from stratigraphical distance. The possibility of Creechbarrow *Sciuroides rissonei* being the ancestor of Eclépens-Gare *S. siderolithicus* suggests that Creechbarrow is earlier than Eclépens-Gare.

Le Bretou has been considered to be slightly younger than Robiac but still Bartonian, on the basis of the occurrence of *Remys minimus*, *Robiacina minuta*, *Xiphodon castrense* and *Simamphicyon helveticus* (Hartenberger *et al.* 1974; Sudre 1978*b*: 185). This is also supported by the presence of *Sciuroides siderolithicus*, probably that recorded as *Suevosciurus* (*Treposciurus*) *mutabilis* by Hartenberger (1973: 65) and as *Suevosciurus* cf. *romani* by Hartenberger *et al.* (1974).

Below is the suggested succession of European Bartonian mammal localities. It conforms with correlation based on other groups.

England	*Paris Basin*	*Switzerland*	*S. France*
			Le Bretou
	Paris?		Robiac
Barton C–F	Berville	Eclépens-Gare	Le Castrais (Lautrec etc.)
Creechbarrow	Paris?		
	Grisolles		
Hengistbury	Sergy/Latilly?		
		Egerkingen β?	Le Castrais (Viviers)?
	Le Guépelle/ Arcis-le-P.	Egerkingen α?	Lissieu?

The solid line indicates the boundary of the two zones and the dashed line the Auversian–Marinesian boundary. The '?' indicates doubt regarding position and, in the case of Paris, two possible positions for the Calcaire de St Ouen specimens are suggested. Other localities like La Livinière in southern France and Laguarrès in Spain are thought to be early Bartonian but have so far yielded sparse mammal faunas, or only endemic taxa or those which are not distinctive of age (see Hartenberger 1973: 67 for lists). *Lophiodon rhinocerodes* and *Palaeotherium r. ruetimeyeri* have recently been recorded from the Grès de Brenne at Fonliasmes, near Poitiers, France (Brunet & Gabilly 1981) and attributed an Auversian age. The two taxa certainly correspond to the *eocaenum–rhinocerodes* Zone but could be either late Lutetian or Auversian.

It is worth noting that the junction of the two mammal zones must be close to the base of the *Rhombodinium draco* dinocyst zone and thus the mammal evidence supports Curry's (1981) proposed modification of the base of the Bartonian.

Evidence from Hampshire Basin sedimentation

West of Whitecliff Bay, the beginning of a series of facies changes from predominantly argillaceous to predominantly arenaceous strata of less marine aspect affects most of the post-London Clay and pre-Fluviomarine strata. The result is that most fossils disappear and dating the western sequences is difficult. At intermediate localities such as Afton, Alum Bay, Barton Cliff and Bournemouth, thinning, facies interdigitation and the persistence of some groups of organisms (e.g. dinocysts) as far west as Bournemouth allows some dating of problem strata from the late Lutetian into the Bartonian (Eaton 1976; Costa *et al.* 1976).

Actual facies change trends are observable at Hengistbury where there is an increase in sand content and abundance of pebble stringers in a westerly direction along the section in the Barton Clay ('Hengistbury Beds') (Hooker 1975). Fisher (1862: 86–88) noted an increase in abundance of pebbles westwards in the basal pebble bed of the Barton Clay at High Cliff, and (1862: 89, figs 3–4) suggested correlation of what is now referred to the upper part of the Boscombe Sands at High Cliff with what is herein referred to lower parts of the Barton Clay Formation in Alum Bay.

Curry (1977), from recognition of two nummulite horizons in the lower Barton Clay (as 'Hengistbury Beds'), correlated an overlying sand at Hengistbury with Bed A3 (High Cliff Sands and Clays of Wright, 1851) at High Cliff and Barton Cliff.

Because of the interruption in the coastal exposure at Poole harbour west of Bournemouth, combined with more facies change and reduction in fossil content, the Creechbarrow sequence is very difficult to match with those further east. The only key seems to be the giant flints which occur at various horizons from *c.* 7 m below the Creechbarrow Limestone downwards. Flints of comparable size are recorded from the Boscombe Sands of Bournemouth (Gardner 1879: 218; Prestwich 1849: 46–47), the slightly diachronous basal Barton Clay pebble/cobble beds at Hengistbury and Alum Bay. They thus appear to occupy a relatively narrow span of strata east of Poole Harbour and it is logical to suggest that they do the same at Creechbarrow. If the Creechbarrow Limestone represents the end of a regression like similar limestones in the later Fluvio-marine series then the stratigraphically closest regression in the marine sequence, sand-

wiched between the Boscombe Sands and Barton Clay Bed D (from faunal evidence; see Text-fig. 67, pp. 246–7) is that of Barton Clay Bed A3. If the progressive reduction of clastic sediment in the Creechbarrow sequence as the limestone is reached represents a raising of the water table resulting from a transgression, then a correlation with Barton Clay Bed B (the nearest transgressive stratum) might be more appropriate.

Palaeoenvironments, palaeoecology and palaeogeography

Depositional environments

The marine province. The Barton Clay and Becton Sand Formations in Christchurch Bay have been shown in the stratigraphical section, pp. 197–212, to have been deposited in a series of three cycles. The erosive base of each cycle is taken to indicate the rapid transgression of a shelf sea, followed by a gradual regressive (progradational) phase, ending in shoreface sands.

At the western end of Christchurch Bay at Friar's Cliff and Hengistbury, there is evidence in lower parts of the sequence of two more cycles. These occur in the upper part of the Boscombe Sands, which here underlie the Barton Clay Formation.

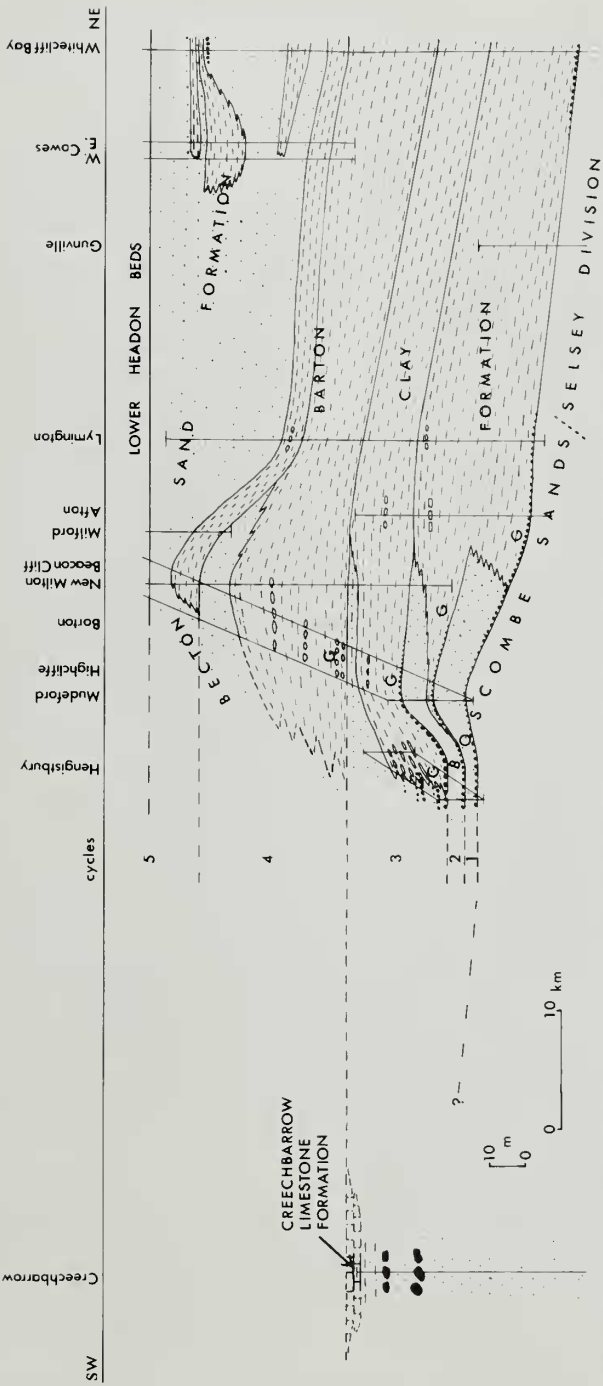
The upper of these cycles has a basal pebble bed and passes from non-glauconitic clayey sand to non-glauconitic sand, both with *Ophiomorpha* and plant debris. At Hengistbury this cycle spans Boscome Sands beds 2 and 3 (Hooker 1975: fig. 3). At Friar's Cliff it spans the 'Highcliff Sands' of Gardner from the pebble bed upwards (see Hooker 1975: fig. 2) or beds 2 and 3 of Fisher (1862: 87, fig. 2).

The lower of these cycles at Hengistbury has a basal pebble bed, resting on laminated lignitic clays and consists almost entirely of light non-glauconitic sand with *Ophiomorpha*, with an impersistent seam of pipe-clay at the top (Boscombe Sands bed 1 of Hooker, 1975: fig. 3; the underlying '?Bournemouth Marine Beds' were incorrectly identified). Only the upper part of this cycle is exposed at Friar's Cliff, where it consists of a thicker unit of light-coloured sands ('Highcliff Sands' of Gardner below the lower pebble bed shown in Hooker 1975: fig. 2). The equivalent in Alum Bay is considered to be the sands of bed 28 of Prestwich (1846).

When traced eastwards these sandy units successively pass laterally into glauconitic sandy silts and silty clays of lower parts of the Barton Clay Formation (Huntingbridge division, including Elmore Member in part). The latter at Afton and Whitecliff Bay seem to continue up into time-equivalents of the lower part of the lower cycle of the Barton Clay in Christchurch Bay, entirely within Elmore facies. They cannot here be subdivided into cycles. These recognition problems are likely to be because successive cycles, up to the lower one of the Barton Clay in Christchurch Bay, transgress each other. The progradational (regressive) phases of the first two did not develop seaward sufficiently to cause facies changes in the more offshore sequence further east (e.g. Afton and Whitecliff Bay). The cycles will here be numbered 1 to 5. The lower, middle and upper of the Barton Clay and Becton Sand Formations in Christchurch Bay, described on pp. 206–7, are numbered 3, 4 and 5 respectively. The lower and upper of the upper part of the Boscombe Sands are numbered 1 and 2 respectively. See Text-fig. 68 for the model.

The glauconitic facies of the cycles are best developed in the west of the area (Christchurch Bay, Alum Bay). Glauconite is considered to form in the sea under conditions of some turbulence, with low sedimentation rates and some organic matter (Reineck & Singh 1980: 151). Porrenga (1967) noted that it was being formed today in the tropics at depths of 125–250 m, controlled by temperature (10°–15°C). However, Bell & Goodell (1967) recorded authigenic glauconite in shelf environments at various latitudes, ranging in depth from 20–1780 fathoms (= 37–3255 m), being formed often inside foraminiferid shells or replacing coprolites or mica flakes; they found that it tends to form in a band parallel to the coastline.

Murray & Wright (1974: 50–51), on the basis of foraminiferids, considered beds B–E at Barton Cliff (glauconitic beds of cycle 4) to have formed under water 50–100 m deep, and beds A2 and F–lower H (non-glauconitic clays of cycles 3 and 4) no deeper than 50 m. Lower and higher strata were referred to an intertidal or estuarine environment and they concluded that 'the Barton Beds at their type locality represent a full marine cycle from continental deposits,



Text-figure 68 Somewhat schematic slice section of Hampshire Basin Bartonian strata, trending approximately north-east/south-west, to show facies distributions and cycles. Vertical bars or oblique windows indicate extent of recorded strata at a given locality. Where present the base of the Lower Headon Beds has been used as the top horizontal datum. For key to lithological symbols, see Text-fig. 2, p. 201. Sources of data: Curry (1942), Hooker (1975), Prestwich (1846) and Whitaker (1910, 1917).

through marsh, inshore and offshore shelf, and back to shallow water conditions'. The close lithological, and to an extent faunal, similarities between cycles 3 and 4 suggest that their 'full marine cycle' may have been repeated. The uniqueness of their agglutinated foraminiferal fauna from A1 (suggesting to them hyposaline tidal marsh) by their own admission takes no account of either the absence by leaching of calcareous fossils in this bed, or the probable absence of agglutinated forms from glauconitic beds in cycle 4 by disintegration on burial (Murray & Wright 1974: 48, 50). See also comments by Curry (1977: 404).

Burton (1933) noticed that certain molluscs occurred in the Lower and Upper Barton Beds, but not in the Middle. These are in fact almost entirely restricted to the sands and clayey sands of Beds A3 and H and thus predominate at homologous stages in cycles 3 and 4. Representative species are: *Vepricardium porulosum*, *Glans oblonga*, *Calliostoma nodulosum*, *Homalaxis* sp., *Cordieria semicostata* and *Tornatellaea simulata*. The very rare brachiopod *Argyrotheca piperipyxis* has a similar distribution. The gastropod genus *Terebellum* also has a similar occurrence but is represented by different species (*T. fusiforme* in A3; *T. sopitum* in upper H). Further repetitions occur between the sandy parts of cycles 4 and 5, e.g. *Glans oblonga* at Barton. Further east this extends also to *Chama squamosa*, *Vepricardium porulosum*, *Crassatella tenuisulcata* and *Terebellum sopitum*, which occur in cycle 5 in Whitecliff Bay. This list is from Gardner *et al.* (1888: 605) who called the horizon at Whitecliff Bay the 'Chama Bed', but according to the dinocysts (Bujak *et al.* 1980) and the lithostratigraphy it belongs to cycle 5. The true Chama Bed of Wright (1851) at Barton belongs to cycle 4.

There are conflicting ideas on water depth in lower parts of the sequence in the east of the area. Murray & Wright (1974: 21) could find no foraminiferans in most of the weathered, poorly-exposed cliff section in Whitecliff Bay and, from the descriptions of the succession by Gardner *et al.* (1888) and White (1921*a*), concluded that clays above the *N. prestwichianus* bed represented 'a return to intertidal, fluvial marsh, and channel environments'. This interpretation is not corroborated by the fully marine mollusc faunas from the 'Chama Bed' (Gardner *et al.* 1888) or in blue clays with *N. rectus* (personal observation). Likewise, the Elmore Member (Fisher beds XVIII–lower XIX) was considered to be intertidal (Murray & Wright 1974: 21), whereas an almost identical lithology (beds S–W) at Fawley (Curry *et al.* 1968: 195) was considered to have accumulated in deeper water than had the Selsey division (beds B–R) and under low oxygenation conditions with limited current movement, which were unfavourable to a rich benthos, in particular molluscs.

It is probable that cycles 3 and 4 represent upward shallowing sequences from richly (more onshore shelf) or poorly (more offshore shelf) glauconitic greenish clays and silts (50–100 m depth) through non-glauconitic blue or grey clays (maximum 50 m depth) to (in the west only) lower shoreface sands (with *Solen*, *Panopea*, *Pinna*, see Curry 1977, and possibly *Ophiomorpha* in cycle 3). Cycle 5 represents a similar upward shallowing sequence but from non-glauconitic clays (*c.* 50 m depth?) through shoreface sands to shelly storm washover sands (at Barton Cliff, Plint 1984). Both molluscs (Gardner *et al.* 1888: 592) and foraminiferans (Murray & Wright 1974) in the upper sandy part of the clays indicate the beginning of a major salinity reduction towards the brackish and freshwater environment of the overlying Lower Headon Beds which conclude cycle 5. At this same lithological horizon in Whitecliff Bay, however, the salinity appears to have been more normally marine with the 'Chama bed' type fauna mentioned above.

At Barton Cliff archaeocetes are known from both the glauconitic and non-glauconitic clay facies and these presumably lived or at least died in this environment. The few land mammals are mainly medium- to large-sized, probably a feature of collecting availability and bias; the bat (p. 242) is an unusual exception, found admittedly by sieving techniques, this group being very rare in marine sediments and rare even at Creechbarrow. The skull of *Plagiolophus curtisi* is unusual in having the cranium and mandible in association, indicating a fairly nearshore site of deposition.

The non-marine province. Knowledge of this province is restricted to strata on Creechbarrow Hill. The sands, clays and conglomerates beneath the Creechbarrow Limestone Formation are poorly exposed and little knowledge has been gained of sedimentary structure. Nevertheless the

poor sorting, the occasional conglomeratic horizons, and the unrolled state of the flints (indicating a nearby source) all suggest that they may be distal alluvial fan deposits (see Blissenbach 1954, Hooke 1967, Reineck & Singh 1980).

A different and more complex depositional interpretation is required to account for the various features of the Creechbarrow Limestone. Indications of three different environments have been found:

1. Fluvial: a. abundant quartz grains in an otherwise fine-grained limestone;
   b. terrestrial mammal remains showing evidence of water transport (see below);
2. Lacustrine: a. freshwater gastropod molluscs;
   b. cyanophyte algal oncoliths often with laminae thin on one side;
   c. calcareous ?chironomid tubes associated with the algae;

(Evidence of either fluvial or lacustrine aquatic environment is given by pantolestids, chelonians, crocodilians, characoid fish (Gaudant 1979), unionids and quartz-grain tubes of ?Trichoptera).

3. Terrestrial: a. ?insect burrows (for aestivation, hibernation or pupation etc.);
   b. land snails and slugs;
   c. well-preserved associated teeth of terrestrial mammals showing little evidence of predepositional transport.

Examples from each of the three groups can be found together in the same hand specimen, so it is unlikely that the disturbed nature of the strata with consequent mixing of layers of different environmental composition can account for this phenomenon. Although a water body of some sort is definitely suggested, there is no evidence that this was very deep. In fact the rarity of pantolestids, crocodilians and chelonians (and small size of the last two, ?juvenile), normally abundant in the vertebrate faunas of the dominantly fluvio-lacustrine (Insole 1972) Headon and Osborne Beds, Bembridge Marls and Hamstead Beds, suggests that it may not have been deep enough to support such a community. Alternatively, their potential food supply might have been excluded by cyanophyte-produced toxins (see Shelubsky 1951).

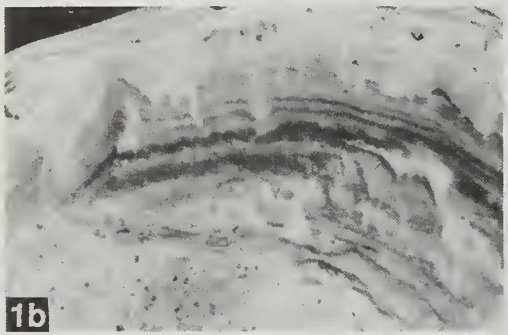
i. Notes on aspects of the biota. Cyanophyta: Recent fluvial and lacustrine cryptalgal structures have identical morphology, according to Jones & Wilkinson (1978), but if only infrequently agitated by waves or currents as in a lake, their banding is thinner on the side of the oncolith in contact with the substrate. Some of the Creechbarrow oncoliths show this form (Hudleston 1903: pl. 11, figs 2–4). In temperate climates (Lake Michigan) Jones & Wilkinson noted a seasonal growth pattern, with most activity in the summer, causing annual layers. In subtropical climates (Florida Everglades) a more complex pattern is produced by short wet and dry periods superimposed on overall wet summer and dry winter seasonality (Monty & Hardie 1976). The Creechbarrow cryptalgal structures are laminated irregularly and in places show scattered branched and unbranched radial filaments (Pl. 35, fig. 1c). In gross structure they are nearly all oncoliths ranging from a few millimetres to a few centimetres in diameter. Most commonly they encrust the fresh-water snail shells (Preece 1980*a*: pl. 4, figs g, h), but they also occur without an obvious nucleus or as apparently hollow cylinders, now filled with limestone matrix and perhaps once formed round twigs, stems or roots, growing or loose (Pl. 35, figs 1–2). One in particular is a straight symmetrical cylinder with faint longitudinal striations on the inside wall and with the encrustation recrystallized to radiating fibrous calcite crystals which give the outer surface a knobbly appearance (Pl. 35, fig. 2). Only one fragment of cushion-shaped stromatolite has been found. When complete it would have been no more than about 10 cm across and it appears to have had more than one gastropod nucleus. Daley (1974) described well-preserved material of two new genera of encrusting cyanophytes from the brackish Bembridge Marls of the Isle of Wight.

?Trichoptera larval cases (Pl. 35, fig. 3): Both specimens are fragments of curved wall composed of a mosaic of subangular quartz grains 0·2–0·8 mm in diameter. They had formed nuclei for algal growth and were only discovered by random breakage in processing (or subaerial weathering) of oncoliths. The curvature suggests an original diameter of *c.* 4 mm. The larger of the two fragments has an incomplete minimum length of 6 mm. Polychaetes (e.g. *Sabellaria*) are

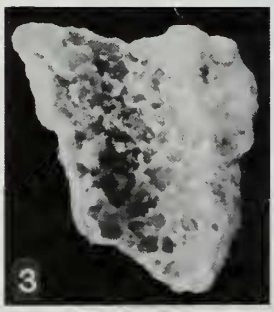
1a

2a

2b


1b

5a


3

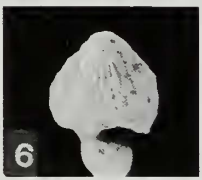
5b

1c

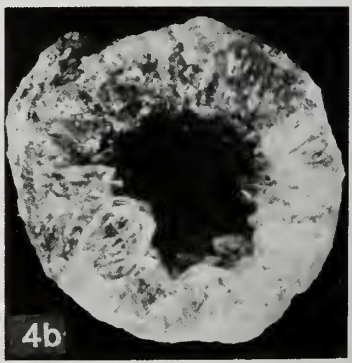
5c

4a

7


6

8


4b

known to construct similar tubes but have generally not become established in fresh-water environments (Chamberlain 1975). Vialov & Sukatsheva (1976) have reviewed the geological record of caddisfly larval cases. Organic-walled types are known from the Palaeogene of western Europe in the Middle Eocene of Geiseltal (D.D.R.) (Haupt 1956) and the Palaeocene of the Isle of Mull (Zeuner 1941). Caddis larvae that construct sandy tubes are more typical of lotic (e.g. fluvial) environments, although some occur in more lentic areas (e.g. lakes) (Chamberlain 1975). Whereas there is insufficient evidence to assign these fragments to Trichoptera with certainty, there is nothing about the specimens to prevent such an attribution (personal communication, P. Barnard 1982).

?Chironomidae larval tubes (Pl. 35, fig. 1b): Randomly orientated, calcite-lined, sparite-infilled tubes occur within oncoliths. Similar structures in marine Triassic stromatolites have been described as the problematicum genus *Microtubus* Flügel 1964, a probable polychaete (see also Wright & Mayall 1981). Modern associations of chironomid larvae and cyanophytes led Anadón & Zamarreño (1981) to recognize as chironomids similar tubes in non-marine Palaeogene oncoliths from Spain. In a modern fresh-water environment with cyanophytes, chironomids are the most likely producers of such tubes, but there is limited morphological support for this attribution (personal communication, P. Cranston 1982).

?Insect burrows (Pl. 35, fig. 4): These also occur in the Bembridge Limestone, where they were originally described as eggs of either turtles or the land snail '*Bulimus*' *ellipticus* (Edwards 1852). White (1921*a*: 117) called them ovoid concretions. Keeping (1910) was the first to record them from Creechbarrow. Preece (1980*a*: 177) called them oviform bodies and compared their spiral grooves to 'the mandibular pattern present in wasp nests'. Their calcite composition appears to constitute a geodal filling of a cavity. Ratcliffe & Fagerstrom (1980) noted that cydnid hemipterans make cell-shaped burrows without access shafts and several other insect groups make vertical or oblique burrows with ovoid terminal cells (trace fossil *Amphorichnus* Myannil 1966). None of the Creechbarrow or Bembridge Limestone bodies appear to have had an access shaft and their orientation in the rock is not recorded as they are normally found weathered out. Their presence nevertheless appears to suggest subaerial conditions.

Tubular burrow: A single slightly flexed tubular limestone burrow fill with no surface structure has been found. It is 45 mm long with a diameter of 10–12 mm.

Fresh-water molluscs: Daley (1972*a*: 27), reviewing earlier studies, stated that *Viviparus* and *Melanopsis* (probably a modern analogue of *Coptostylus*) live today in rivers, ponds, lakes and canals, grazing bare, soft bottom muds. He noted that whereas *Melanopsis* appears to prefer areas free from aquatic vegetation, *Viviparus* will live in marshes; and that whereas *Viviparus* is sensitive to salinity increases above 3‰, *Melanopsis* is tolerant of brackish and fresh water. The occurrence of *Viviparus* at Creechbarrow is an important indication of fresh water, although the abundance of *Coptostylus brevis* suggests near optimum conditions for this species. Preece

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Plate 35 Light macrographs of miscellaneous Creechbarrow biota. Figs 1–3, 4b are not sprayed with ammonium chloride.

Fig. 1a–c Transverse section of cyanophyte oncolith (V.61740); a, complete view of polished face, showing concentric laminae and thinning on one side, × 1; b, details of laminae and associated ?Chironomidae tubes, × 4; c, filaments (one branched), × 500.

Fig. 2a, b Regularly cylindrical oncolith recrystallized to radiating acicular crystals but with a few concentric laminae remaining (V.61741); a, side view, × 1·5; b, polished face, × 3.

Fig. 3 Fragment of oncolith coating part of ?Trichoptera larval case, composed of sand grains, (In.64609), viewed from inside, × 6.

Fig. 4a, b ?Insect burrow (GG21472); a, side view, × 2; b, broken end showing geodal calcite infilling, × 4.

Fig. 5a–c Tooth of characoid fish (P61171), × 7; a, buccal view; b, occlusal view; c, lingual view.

Fig. 6 Crocodilian tooth (R10006), × 5·5.

Fig. 7 Bone fragment of indeterminate ?mammal with gnaw marks (M37572), × 6·5.

Fig. 8 Fragment of mammalian scapula with gnaw marks (M37573); medial view with glenoid to left, × 3.

(1980*a*: 178) suggested poorly vegetated or bare lime mud surfaces to account for the abundant assemblage of *Coptostylus*, the absence of Planorbidae and near absence of Lymnaeidae.

Absence of ostracods and charophytes: This may be diagenetic rather than original. Recrystallization in the limestone has destroyed the fine detail on the larger shells and it is likely that small calcareous organisms would have been obliterated completely. See also comments by Preece (1980*a*: 178).

ii. Problem of distinction of stromatolites from calcretes. This subject has been discussed by Read (1976). Insole (1972) described various limestones in the Osborne Beds and Bembridge Limestone, which he considered to represent calcretes. In the case of the limestone in the Osborne Beds at Headon Hill, a sequence of marls passing up through nodular limestone is superficially similar to that at Creechbarrow. The Creechbarrow sequence differs in the presence of oncoliths rather than nodules. The limestones themselves also differ. The limestone in the Osborne Beds is vertically fissured and brecciated and the cavities have surface rinds, which is consistent with the structure of calcretes (see Hay & Reeder 1978). Goudie (1973: 23) noted that an important component of calcrete is silica (average 12·3%), including both quartz grains and amorphous silica cement. The Creechbarrow Limestone, in its lack of brecciation, fissuring and amorphous silica cement (the latter was not found in insoluble residues – see methods section, p. 194), is more consistent with an algal than a calcrete origin for the oncoliths. It cannot be excluded, however, that above the modern erosion plane at Creechbarrow, higher parts of the succession now missing may have shown evidence of pedogenesis. This can be associated with terminal regressive phases of lacustrine sequences (e.g. Engesser *et al.* 1981, Goudie 1973) and could account for the recrystallization and poor or non-preservation of small calcareous fossils in the Creechbarrow Limestone.

iii. Conclusions. Preece (1980*a*) discussed the contrasting views of Hudleston (1902*a*), who thought the Creechbarrow Limestone represented deposition in a lake, and Bury (1934), who considered it a swamp, and partially favoured Bury because of the rarity of land shells in modern lake deposits. Bury was comparing the Limestone with the nearby Holocene tufa of Blashenwell. Preece (1980*b*) concluded that the Blashenwell tufa was deposited on marsh-ground with some water flow and boggy pools. In his list of recorded gastropods, nearly all are terrestrial and none are totally aquatic, a situation different from Creechbarrow. Moreover, his suggestion that 'the nodular or pisolitic lithology and even encrustation of gastropod shells is suggestive of flowing water or seepages' is not corroborated by Jones & Wilkinson (1978), who demonstrated that pisolitic growth can take place, admittedly at a slower rate, on the underside of the body in contact with the sediment.

Several of the features of the Creechbarrow Limestone are consistent with environments found in the 'interior marshes' of the Florida Everglades (see Monty & Hardie 1976). Modern environments in this area have several times been invoked as possible analogues to various late Eocene/early Oligocene deposits of southern England (e.g. Machin 1971, Keen 1977, Collinson 1983). Salient points drawn from Monty & Hardie (1976) which fit the data from Creechbarrow are: the total fresh-water nature of the area; rainy summers and dry winters with superimposed smaller scale wet and dry periods favouring growth of cyanophytes but discouraging aquatic higher plants; cyanophytes able to grow in depths from a few cm to a few tens of cm; environment very quiet. The main features which do not fit the data from Creechbarrow are: the more continuous nature of the algal mat; the absence of sandy detrital deposition; and the calcareous nature of the bedrock substrate. At Creechbarrow the calcium carbonate is likely to have been derived from erosion of nearby Chalk, as the unworn flints and derived Bryozoa (p. 420) testify; the more restricted growth of algae and the detrital elements suggests that the environment was only intermittently quiet.

A Palaeogene non-marine to paralic complex in the Ebro Basin, Spain, with one facies similar to that at Creechbarrow, has been described by Anadón & Zamarreño (1981). This was interpreted as a 'palustrine setting in relation to alluvial fans'. The facies consisted of calcareous mudstones and argillaceous or sandy limestones; the algal bodies were mainly small asym-

metric oncoliths (up to 3 cm in diameter and 10 cm in length) with chironomid tubes. This was interpreted as representing marshes and shallow lakes, strongly influenced by sheet floods from the alluvial fans.

Thus it is possible to envisage for Creechbarrow a shallow fresh-water lake to marsh environment, moderately favourable to the growth of oncolitic cyanophytes and to the existence of mud-browsing gastropods and unionid bivalves. This would be subject to periodicity: a, flooding, which introduced clastic detritus and land-derived vertebrates as thanatocoenoses; and b, lowering of the water level, which inhibited algal growth and provided emergent marginal areas which were burrowed by insects and colonized by land gastropods and presumably some land plants.

The environment of deposition between Creechbarrow and Hengistbury will remain unknown as modern erosion has penetrated to much lower strata over the whole area. However, the evidence of progradation of coastal sand in the upper part of the cycle 3, and brackish elements in the otherwise typically marine A3 fauna in Christchurch Bay, e.g. *Theodoxus* spp., *Paludestrina* sp., *Melanopsis* cf. *subfusiformis*, *Batillaria* cf. *calcitrapoides* and *Potamides* cf. *variabilis* (see Burton 1933), suggests that there may have been an intervening hyposaline lagoon.

Tectonic hypothesis. Alluvial fans are known to develop from abrupt topographical features, often fault scarps (Reineck & Singh 1980: 298). If the poorly sorted sands, clays and conglomerates beneath the Creechbarrow Limestone are correctly interpreted as alluvial fan deposits (see above), then we might expect some such feature to have existed in Bartonian times, roughly to the west of Creechbarrow.

Faulting is present in east Dorset south of Creechbarrow in the form of the Ballard Down Fault which trends east–west through the Isle of Purbeck. Small (1980: 52, fig. 1) intepreted this as having been active before the deposition of the Creechbarrow Limestone, on the grounds that 'Creechbarrow type' flints occur in solution hollows in the Chalk south of Creechbarrow. He thus ignored Arkell's (1947: 241) *caveat* that the flints could have been redeposited long after initial deposition in the Eocene.

East–west *en echelon* folds affecting the Hampshire Basin Palaeogene deposits have been attributed by Shearman (1968) to NW–SE dextral wrench faulting in the Palaeozoic basement, following pre-existing joint directions, which can be seen at the surface today in Devon and Cornwall. For details of these structures in SW England see Dearman (1964) and Palmer (1975), and references therein. Shearman considered that the movements in the basement were transmitted upwards into the Mesozoic and Cainozoic cover in the form of these folds accompanied by a décollement. He repeated an experiment by Pavoni (1961) in which wet tissue was placed over two boards. When the boards were slid past each other dextrally in a SE direction, *en echelon*, sigmoidal folds trending east–west were produced in the tissue across the line of displacement. No northerly inclined asymmetry, as occurs in the Hampshire Basin, was produced, but Shearman accounted for this by décollement, which did not occur in the experiment.

All these authors accepted a Neogene date for the faulting and folding, i.e. long after deposition of the Creechbarrow Limestone. Important lines of evidence are: 1, the youngest beds preserved in the Palaeogene sequence (Oligocene Hamstead Beds) are affected by the east–west striking folds; 2, the Oligocene deposits of the Bovey Basin are affected by NW–SE dextral wrench faulting; and 3, penecontemporaneous Palaeogene folding and facies lineation in the Hampshire and Paris Basins have a NW–SE trend (see Fig. 69; Murray & Wright 1974: figs 25E–F, 28; Daley & Edwards 1971; Pomerol 1967). This argues against the model of Small (1980) and suggests that a NW–SE trending feature in the area of central Dorset may have propagated the Creechbarrow fans. No superficial faults of this trend have been detected in this area but a feature of similar orientation occurred a little further to the east in late Albian and Cenomanian times. This is known as the Mid-Dorset Swell. It caused a drastic thinning of deposits and hardgrounds in its vicinity and its existence has been attributed to movements in Palaeozoic basement structures (Drummond 1970). Plint (1982) has provided sedimentological evidence in support of Eocene activity along the east–west fault and fold axis of Purbeck and

the Isle of Wight. His evidence, however, could equally be used to support a NW–SE fold structure, which would better fit the other evidence. Moreover, his palaeocurrent direction for M. Eocene meandering rivers is to the north-east (Plint 1983: fig. 12).

If NW–SE normal faulting with downthrow to the NE had occurred in the Palaeozoic basement in later Eocene times in central Dorset, slightly SW of the Mid-Dorset Swell, a NE-dipping monocline would have been produced in the Mesozoic and Tertiary cover. The monocline would have been obliterated by the much severer folding and faulting of the Neogene. Such a tectonic model could not only account for the Creechbarrow alluvial fans but also the successive rapid marine transgressions by intermittent activation of the monoclinal structure causing subsidence on the down-dip side. The clastics would thus have been available to fill much of the marine as well as the alluvial part of the basin between each transgression.

The glauconitic nearshore facies is more restricted in the Barton Clay Formation than in the Bracklesham Group. Deeper water clays are reached more rapidly in an offshore direction and facies change takes place over a shorter distance (e.g. interdigitation of J with K over a distance of *c.* 1 km at Barton). Moreover, the braiding of the rivers presumed to have formed the alluvial fans contrasts with the meandering rivers considered responsible for the earlier fluvial western facies coeval with the marine Bracklesham Group (Plint 1983). All this suggests greater topographic relief, a more rapidly prograding shoreline with a steeper palaeoslope, and stronger current action during early stages of the cycles. See Text-fig. 69 for Hampshire Basin Bartonian facies map.

If Shearman's experiment is repeated with the NE plank at a slightly lower level than the other, simulating primary normal faulting, the folding produced by secondary dextral wrench faulting is overturned to the north on the downthrow side. This simulates the asymmetry of the Purbeck monocline without the necessity of a décollement.

Palaeoecology of the Creechbarrow mammal fauna.

Introduction. The restricted total outcrop, poor exposure and disturbed state of the Creechbarrow Limestone Formation make most aspects of taphonomic and palaeoecological analysis difficult or impossible. On the positive side, unlike most other English Palaeogene deposits, no surface collecting could be done and all but three specimens, found during excavation work, were recovered by systematic sieving techniques. Of the matrix collected, about 1600 kg has been completely processed (with the exception of the larger limestone fragments), the remainder being initially searched for only larger mammalian specimens. The proportional abundances of the mammal specimens recorded from this 1600 kg sample can therefore be viewed with some confidence. Immediate areas of bias are likely to be against: 1, those mammals without teeth like the pangolins (Pholidota) and anteaters (Xenarthra), both of which are known from the Lutetian of Messel, W. Germany (Storch 1978, 1981), but unknown at Creechbarrow (see p. 441); and 2, the larger herbivores and carnivores because of the restricted outcrop and poor exposure (see p. 207). Less accountable problems are the impossibility of knowing how accurately the fossil sample reflects the composition of the living assemblage. For a review of these types of problems and bias in assessing modern mammalian populations, see Western (1980).

Preservation. The mammal remains consist predominantly of teeth with relatively few bony skeletal parts being found. The teeth range in appearance from fresh, with mahogany-coloured enamel and slightly darker dentine, to worn and battered with an overall dark brown colour. Some apparently unabraded teeth are almost white; these seem to belong to the first preservational category, but recent weathering has leached them. Manganese is frequently found coating the teeth and is probably also responsible for the dark staining. In preservation bones range from unworn but weathered and white, to worn and of a dark brown colour. Some bones can be worn and light-coloured and have probably undergone leaching like the light-coloured teeth. No preservation is restricted to any particular taxon unless it happens to be very rare or unique.

It is considered that, whereas fluvial transport probably brought most of the specimens into the depositional environment, the more worn and dark-coloured specimens have been carried

Text-figure 69 Map of Hampshire Basin Bartonian facies and palaeogeography. 1 = hypothetical north-east dipping monocline; 2 = postulated position of maximum shoreline; 3 = probable south-west limit of glauconitic beds; 4 = known (continuous) and extrapolated (dashed) south-west and north-west limits of Barton Clay bed J (and lithological equivalents away from Christchurch Bay); 5 = postulated north-eastern limit of regressive sands of cycles 1 to 3; 6 = postulated easterly limits of Becton Sand bed 1 (and lithological equivalents away from Christchurch Bay). Sources of data: Curry (1942), Hooker (1975), Reid (1898, 1902*a*, *b*), Whitaker (1910, 1917) and White (1921*a*, *b*).

some distance, whilst the fresher specimens probably died much closer to the depositional site. A scatological origin is thought to be unlikely or at least an unimportant factor for two reasons. Firstly there is a complete gradation between the end members of the two preservational types, suggesting continuously varying distances of origin. Secondly the worn appearance of the tooth crowns coincides in most cases with loss of roots, indicating fluvial transport (see Korth 1979), and differing from the enamel-less but rooted teeth considered by Fisher (1981*a*, *b*) to have been excreted by crocodilians. This accords with the rarity of crocodilians at Creechbarrow. Moreover, the preservation lacks the characteristic corrosion typical of certain avian predators (Mayhew 1977).

Some of the better-preserved teeth have been found to be associated, according to their matching interstitial facets as well as their similar natural wear and preservation (e.g. *Lophiotherium siderolithicum* M36177 and M37705, p. 351; and *Haplobunodon venatorum* M37716 and M37529, p. 405). M^{1-3} of *Dacrytherium elegans* (M37177, p. 410) were found in a row, but slightly separated from one another and without the jaw, in a block of limestone. The main specimen of *Plagiolophus curtisi creechensis* (M36181, p. 364) consists of associated upper and lower jaws on both sides as well as numerous unreconstructable jaw fragments. It seems a remarkable coincidence that one of only two specimens of the same species from the marine Barton Clay should also have both upper and lower jaws associated. Single teeth in jaws have occurred in two cases: *Haplobunodon venatorum* (M37544, p. 408) found in the field; and *Gesneropithex figularis* (M35407, p. 234) found separated in residues, but where the broken root surfaces on tooth and jaw were found to match up. The few other jaws found were all edentulous and this condition may be due largely to recent weathering of the deposit.

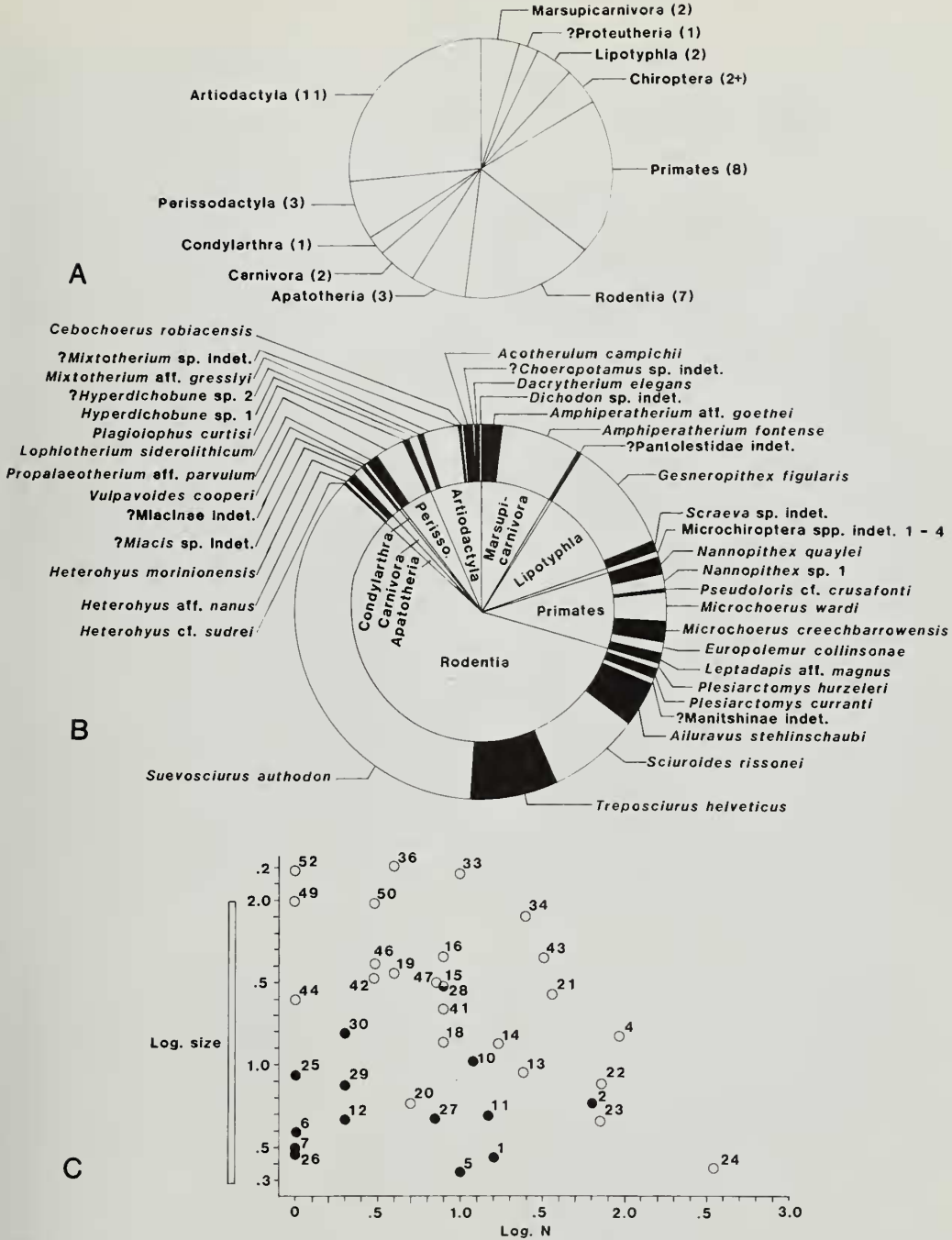
Three isolated teeth have been found in limestone blocks. They belong to *Plesiarctomys curranti* (M35450, p. 285; Pl. 13, fig. 7), *Lophiotherium siderolithicum* (M37446, p. 351) and *Acotherulum campichii* (M36802, p. 400). All are dark-coloured, battered and rootless.

Some of the bones (both fresh and worn) show evidence of rodent gnawing (Pl. 35, figs 7–8). In some cases the marks are transverse to the long axis and occur as parallel grooves; in another they occur round a bite notch (see Bonnichsen 1979 and Morlan 1980 for modern examples). Those on a scapula fragment (Pl. 35, fig. 8) are of appropriate size for the incisors attributed herein tentatively to *Suevosciurus authodon*. Those figured in Pl. 35, fig. 7, however, appear to have been made by much smaller teeth. If these were of a rodent, it must have been smaller than any recorded from teeth at this locality.

Faunal Composition. Text-fig. 70A–B shows relative abundances based on the ordinal composition of species and individuals respectively. They show that whereas the artiodactyls display the greatest diversity of species, the rodents make up over 50% of the individuals (more than a third belonging to *Suevosciurus authodon*). The apatotheres, whilst showing some diversity, are few in number of individuals. They were also found to form only *c.* 1% of North American Eocene faunas (West 1973). Creechbarrow seems notable for having representatives of groups normally rare in European Eocene deposits, i.e. one paroxyclaenid, three apatotheres, two *Plesiarctomys* and a third undet. manitshine, and *Ailuravus*. This may be more a feature of the bias against smaller mammals in old collections from the main Lutetian and Bartonian localities and the increasing rarity of these groups from late Bartonian times onwards. The latter feature is particularly relevant to the locality of Robiac.

Text-fig. 70C shows log. of maximum numbers of specimens per species for the 1600 kg sample plotted against log. of size based on M^1 area (or the best approximation to it when this tooth was not available). Creighton (1980) showed that area (length × width) of M_1 correlated accurately with body size in modern mammals (except edentates). M^1 is preferred here because length and width are usually approximately equal and can thus be more easily extrapolated, when only lower teeth are available. In certain mammals, e.g. rodents, M^1 and M^2 are essentially the same size and their mixing for statistical purposes still produces a low coefficient of variation.

In Text-fig. 70C, species considered on their dental morphology to be at least mainly frugivorous or herbivorous plot in broad linear fashion, becoming less abundant with increasing



Text-figure 70 Diagrams of relative abundances of Creechbarrow mammals.

A. Circular diagram showing proportional representation of species numbers per order.

B. Circular diagram showing proportional representation of specimen numbers per species, grouped by order.

C. Scatter diagram of log. size (based on M^1 area, or its extrapolation by squaring M_1 length) against log. numbers of individuals (based on maximum numbers of teeth). Bar on left gives range of size of modern arboreal herbivores from Eisenberg (1978) extrapolated to tooth size using Creighton (1980). Outline circles are probable herbivores; solid circles are probable insectivores/carnivores; numbers against symbols refer to taxa listed in Table 1, pp. 212–215.

size. Those species considered on dental morphology to be mainly insectivorous or carnivorous are rarer in occurrence than the equivalent-sized herbivores. There is some overlap, however, the herbivorous ?*Mixtotherium* sp. indet. and cf. Manitshinae indet. being exceptionally rare and the carnivore ?*Miacis* sp. indet. and possible carnivore *Amphiperatherium fontense* being relatively common.

The correlation of increasing rarity with increasing size in the herbivores may reflect generally more scattered populations of animals with greater biomass, or it might reflect their lower birth and death rates (see Western 1980). This ignores possible gregarious versus non-gregarious habits, simple rarity or abundance of particular species, range of habitats sampled and many other unknowns. However, as a general rule, insectivore-carnivores tend to be rarer than frugivore-herbivores for a given size (Wolff 1975). Moreover, the consistency in the range of good to poor preservation for all the taxa suggests that even if areas at different distances from the depositional site have been sampled, the same fauna occurred throughout.

The correlation of herbivore size and abundance plus the presence of the rhinoceros-sized herbivore *Lophiodon* cf. *lautricense* in nearly contemporaneous marine deposits at Hengistbury suggest that larger herbivores and probably carnivores may once have lived in association with the Creechbarrow fauna as known at present, but are missing on account of inadequate sampling. The range of larger perissodactyls and artiodactyls as well as the larger creodonts and carnivores present in such Bartonian localities as Eclépens-Gare and Robiac also supports this. If the linear plot of Text-fig. 70C is continued to the log. M^1 area of *L. lautricense* (3·34 calculated from Sudre's 1971 measurements), it can be calculated that somewhere in the region of 30 tonnes of Creechbarrow Limestone would have to be processed in order to find even a single individual of this species (if present).

Korth (1979) determined a sequence of fluvial deposition of different mammalian skeletal elements from settling and flume experiments. Particular elements grouped into five categories. Generally poor preservation of bone at Creechbarrow prevents a direct comparison with his categories, because of the likelihood of bias against those which were small and fragile and those that were large and little transported (i.e. less mineralized and liable to shattering to an unrecognizeable condition). Nevertheless a large range of different elements of different sizes and different preservation states are present. Complete or fragmentary rib (1), radii (2), ulna (1), calcanea (2), femur (1), mandibles (10), tibia (1), metapodials (6), podials other than calcaneum and astragalus (3), phalanges (5) and sesamoids (3), as well as the many teeth, were recovered from the 1600 kg sample. In addition, fragments of a vertebra, pelvis, scapula and astragali have been recovered from other samples.

Notes on diet, habits and habitat. Table 39 lists the Creechbarrow mammal taxa with, for each, a suggested nearest living relative (column 1), modern taxon with similar teeth (if available) (column 2) and where possible a relevant nearest relative from the early Lutetian of Messel, B.R.D., where articulated skeletons often with soft parts and gut contents are known (column 3). In many cases the first column will be irrelevant, particularly in the case of totally extinct family or higher taxa. If, however, this is the same as, or closely related to, the taxon in the second column, the significance of the latter is reinforced. Column 3 is important either as a back-up or in the absence of a column 2 taxon. Comments on the possible ecology of the Creechbarrow mammals are given below, incorporating the Table 39 data.

Didelphidae. Crochet (1980: 230) noted that an arboreal habit predominates in modern didelphids, but some are ground dwellers and one a specialized aquatic. He also noted that their diet is very varied from insectivorous, carnivorous to granivorous and frugivorous, and that whereas there are different dietary specializations between different species, the overlap is great. He suggested (1980: 231–232) that the structure of the humerus in the extinct *Peratherium* might indicate less arboreality than modern forms; but preferred the idea that it reflected some unknown specialization of the European Tertiary forms. He also suggested that the teeth of the genus *Amphiperatherium* showed a tendency towards carnivory.

Table 39 Nearest living relatives and modern dental analogues of the Creechbarrow mammals. The third column gives the relevant nearest relative in the Lutetian fauna at Messel, B.R.D.

Creechbarrow taxon	Nearest living relative group	Modern analogue with some similar teeth	Nearest Messel relative
Amphiperatherium aff. *goethei*	Didelphini	*Marmosa*	
A. fontense	Didelphini	*Marmosa*	
?Pantolestidae indet.	?		*Buxolestes piscator*
Gesneropithex figularis	Erinaceidae?	*Neotetracus*	*Pholidocercus hassiacus*
Scraeva sp. indet.	Erinaceidae?	*Ptilocercus*	
Microchiroptera indet. 1–4	Microchiroptera	most insectivorous microchiropteran families	Microchiroptera
Nannopithex quaylei	*Tarsius*	*Microcebus*	
N. sp. 1	*Tarsius*	*Microcebus*	
Pseudoloris cf. *crusafonti*	*Tarsius*	*Tarsius*	
Microchoerus wardi	*Tarsius*		
M. creechbarrowensis	*Tarsius*		
Europolemur collinsonae	Lemuroidea	*Alouatta*	Adapidae indet.
Leptadapis aff. *magnus*	Lemuroidea	*Hapalemur*	
Adapinae indet.	Lemuroidea		
Plesiarctomys curranti	Rodentia	*Ratufa*	
P. hurzeleri	Rodentia	*Ratufa*	
?Manitshinae indet.	Rodentia		
Ailuravus stehlinschaubi	Rodentia	*Petaurista*, *Trogopterus*	*A. macrurus*
Sciuroides rissonei	Rodentia	*Iomys*	*Masillamys krugi*
Treposciurus helveticus preecei	Rodentia	*Iomys*	*Masillamys krugi*
Suevosciurus authodon	Rodentia	*Iomys*	*Masillamys krugi*
Heterohyus cf. *sudrei*	Ferungulata?	*Dactylopsila*, *Daubentonia*	
H. aff. *nanus*	Ferungulata?	*Dactylopsila*, *Daubentonia*	
H. morinionensis	Ferungulata?	*Dactylopsila*, *Daubentonia*	
?*Miacis* sp. indet.	Carnivora		*Paroodectes feisti*
?Miacinae indet.	Carnivora		*Paroodectes feisti*
Vulpavoides cooperi	Ungulata	see p. 446	*Kopidodon macrognathus*
Propalaeotherium aff. *parvulum*	*Equus*		*P. messelense*
Lophiotherium siderolithicum	*Equus*		*P. messelense*
Plagiolophus curtisi creechensis	*Equus*	*Dendrohyrax*	*P. hassiacum*
Hyperdichobune sp. 1	Artiodactyla		*Messelobunodon schaeferi*
?*H.* sp. 2	Artiodactyla		
Mixtotherium aff. *gresslyi*	Artiodactyla	*Indri*, *Propithecus*	
?*M.* sp. indet.	Artiodactyla		
Cebochoerus robiacensis	Artiodactyla	*Cercocebus albigena* *Cercopithecus pogonias*	
Acotherulum campichii	Artiodactyla	*Cercopithecus pogonias*	
Haplobunodon venatorum	Hippopotamidae?		*Masillabune martini*
?*Choeropotamus* sp. indet.	Hippopotamidae?		
Dacrytherium elegans	Artiodactyla	*Indri*, *Propithecus*	
Dichodon cf. *cervinus*	Camelidae?	see p. 447	
D. sp. indet.	Camelidae?	see p. 447	

Pantolestidae? A semiaquatic mode of life for this family was originally suggested by Matthew (1909) when describing the type genus. This was confirmed by a skeleton of *Buxolestes* from Messel, which has a tail with swimming adaptations and gut contents including fish (Koenigswald 1980*a*). The Creechbarrow specimens are only tentatively referred to the family but may also have been semiaquatic.

Lipotyphla. The cheek teeth of *Gesneropithex figularis* are similar in cusp pattern to those of hedgehogs, but differ in the following important ways: metastylar wing is reduced along with the degree of buccal phase shear; protocone and hypocone crests are better developed along with greater degree of lingual phase wear; cristid obliqua is higher for lingual phase wear; and paracristid is reduced along with general buccal phase shear. The only extant erinaceid where there is any sign of reduction of the metastylar wing and paracristid on the molars is the galericine *Neotetracus*, which has fewer insect and more plant items in the diet than the others (Walker 1975).

A proposed combination of insectivory and frugivory for *G. figularis* from modern dental analogy is supported by the record of plant and insect remains as stomach contents of the amphilemurid *Pholidocercus* from Messel (Koenigswald & Storch 1983: 492). Study of several complete skeletons from this locality led Koenigswald & Storch (1983: 492–493) to conclude that *Pholidocercus* was mainly a waterside ground dweller capable of shallow digging in a moist substrate. *Gesneropithex* is tentatively attributed similar habits, although no postcranial elements are yet known.

Scraeva and other nyctitheres are generally considered insectivorous, but it is difficult to find modern analogues with similar cuspate teeth that are not either nyctalodont or myotodont (Menu & Sigé 1971). The mainly insectivorous (Walker 1975) tupaiid *Ptilocercus* has both anterior teeth and cheek teeth with somewhat similar cusp patterns; but incisor denticulations are missing, intermediate conules are missing on the upper molars and the lower molars are broader, less high-cusped and the cristid obliqua is less oblique. *Scraeva* then appears more distinctly specialized for insectivory than *Ptilocercus*.

Microchiroptera. Nothing more can be said than that the few teeth resemble those of insectivorous modern Microchiroptera and presumably had a similar diet. That there were Eocene insectivorous bats has been shown by Smith *et al.* (1979) for Messel specimens with gut contents.

Primates. The family Tarsiidae, being monotypic and relict today, cannot necessarily be expected to provide information on all the diverse members of the tarsiiform Omomyidae (see Szalay 1976). Of the Creechbarrow microchoerines, only *Pseudoloris* is really similar dentally to *Tarsius* (Teilhard 1921; Szalay 1976). It probably had a similar insectivorous/carnivorous diet. The species of *Nannopithex* have a modern dental analogue in *Microcebus*, which is mainly insectivorous (Walker 1975). *N.* sp. 1 (p. 251), however, unlike *Microcebus* has wrinkled enamel and may show a slight trend towards herbivory. *Microchoerus* was suggested by Szalay & Delson (1979: 265) to be 'primarily folivorous' because of the predominance of sharp cutting edges on its cheek teeth, maintained throughout wear, although they did find it difficult to decide whether the herbivorous emphasis was on fruit or leaves. The late advanced species *M. edwardsi* exhibits much cusp duplication and accessory crests which would fit an adaptation to folivory (cf. folivorous rodents discussed below). Except for the presence of a molar mesostyle, however, early species, as at Creechbarrow, are very similar to *Necrolemur*, which Szalay & Delson (1979: 262) considered 'highly frugivorous'. Postcranial evidence of incipient typical modern tarsier locomotory specializations is scanty but widespread in the Omomyidae, including the Microchoerinae (Szalay & Delson 1979; Schmid 1979). The five Creechbarrow microchoerines are therefore considered arboreal clinger-leapers with the variety of dietary specializations outlined above.

Szalay & Delson (1979: 125) suggested a frugivorous-insectivorous diet for *Europolemur* (then monotypic). *E. collinsonae*, however, shows specializations paralleling those of *Caenopithecus* in buccal flexing of the molar centrocrista and premolar simplification. Szalay & Delson (1979:

143) suggested *Caenopithecus* was a folivore, comparing it with modern indriids. *E. collinsonae*, in its slightly less *Caenopithecus*-like specializations, was probably therefore frugivorous-folivorous. *Leptadapis magnus* was considered by Szalay & Delson (1979: 139) and Gingerich & Martin (1981: 254) to be probably folivorous. Its tooth pattern is somewhat like the modern folivore *Hapalemur* but the upper molars are relatively longer and the hypocones larger, whilst the lower molars have lower metaconid–metastylid and higher entoconid cusps (see Seligsohn & Szalay 1978).

Fogden (1974) found that modern *Tarsius bancanus* inhabited mainly secondary forest with minor occurrence in the understory of primary forest, avoiding forest canopy, very dense vegetation and also rather open secondary vegetation with dense herbaceous cover. Whether or not extinct tarsiiforms had broader tolerances is not known. Koenigswald (1979) has demonstrated the presence of a typical lemuriform hind foot complete with groom claw in a Messel adapid. According to the evaluations of Decker & Szalay (1974) and Gingerich & Martin (1981: 255), it seems reasonable to consider both *Europolemur collinsonae* and *Leptadapis* aff. *magnus* as arboreal.

Rodentia. The dental diversity of the Lutetian–Bartonian rodent radiation is paralleled and exceeded by living members of the Sciuridae. For instance, great similarities are shown by manitshine paramyids to *Ratufa*; ailuravine paramyids to *Petaurista* and *Trogopterus*; pseudosciurids to *Iomys*; and even glirids to *Exilisciurus*.

Wood (1962) considered that the manitshine genera *Manitsha* and *Ischyrotomus* were ground-dwelling and possibly subfossorial, but could not be precise on their individual specializations. Unlike these genera, *Plesiarctomys* is unknown beyond the skull and dentition, so questions of arboreality or ground dwelling are impossible to answer. Its cranial and dental similarities to other manitshines make the latter more likely. *P. curranti* has broadly basined cheek teeth with some enamel wrinkling and nearly transverse buccal and lingual phase mastication. It is thus very similar to *Ratufa* which is mainly a frugivore. *P. hurzeleri* has larger blunt-crested cheek teeth, but both species may have been frugivorous.

Arboreal adaptations have been suggested for Messel *Ailuravus macrurus*, including prehensility of the very long tail (40 vertebrae), by Weitzel (1949). Wood (1976*a*: 146) suggested a frugivorous diet for the genus. *A. stehlinschaubi*, however, has cheek teeth with many more accessory crests and wrinkles than has *A. macrurus*, and in these structures it is similar to modern *Petaurista* and *Trogopterus*. *Petaurista* was considered to have an arboreal rating of 4·5 (out of 5) and a herbivory rating of 3·5 (out of 5) by Eisenberg (1978) and was stated to have a diet of leaves, fruit and seeds by Muul & Lim (1978). *Trogopterus* is recorded as feeding on oak leaves (Walker 1975). *Trogopterus* has slightly higher-crowned and more elaborately selenodont and crested teeth, but is otherwise very similar in pattern to *A. stehlinschaubi*, having upper molar hypocones unlike *Petaurista*. Both modern genera, however, have less transverse motion in both buccal and lingual wear phases, although within the *Sciurus* type (see Butler 1980). It is concluded therefore that *A. stehlinschaubi* was arboreal and essentially a folivore.

Iomys shares with the Creechbarrow pseudosciurids squared upper molars with large hypocone joined by metalophule to the metacone, and lower molars with hypolophulid. Of the three pseudosciurids in the fauna, *Suevosciurus* is closest in molar morphology to *Iomys*, but even so is less lophodont than this genus, and wear is less oblique. *Iomys* has a diet of fruit and seeds (Muul & Lim 1978) so it is probable that *Sciuroides rissonei*, *Treposciurus helveticus preecei* and *Suevosciurus authodon* were also frugivorous/granivorous. *Suevosciurus* is known from an almost complete articulated skeleton (*S. ehingensis*, M. Oligocene of Armissan; Lavocat 1955, as *Pseudosciurus suevicus*). Its fore and hind limb proportions and unfused tibia and fibula suggested to Lavocat a primitive scrambler, capable of living both on the ground and to a certain extent in trees, but with no specific arboreal adaptations. This was probably also the case with *Sciuroides* and *Treposciurus* and appears to have been the primitive rodent condition (Lavocat 1955, Wood 1962).

The later (Oligocene) rather restricted distribution of *Suevosciurus* (mainly in southern Germany) suggests some specialization, but the ability of two lineages of this genus to cross the

'Grande Coupure' virtually unchanged suggests some versatility of habits or the occupation of a niche not exploited by the new immigrants. The drastic reduction of *Sciuroides* at the same time as the spread of theridomyids in the early Ludian does not support the theory that both shared similar ecological adaptations (see Schmidt-Kittler 1971*a*: 125–127). The slightly different emphasis of longitudinal (in *Sciuroides*) versus transverse (in *Suevosciurus*) crests is likely to reflect only minor dietary differences.

Apatotheria. Stehlin (1916) compared the genus *Heterohyus* with the modern lemuroid *Daubentonia* mainly in search of relationship, but in this he has subsequently been shown to be incorrect. West (1973: 23–24) compared *Apatemys* teeth functionally with those of the phalangerid *Dactylopsila* and concluded that like the latter it too may have been arboreal and used its enlarged incisors for tearing bark open to hunt for insects. Cartmill (1974) compared skull structure in relation to food-gathering function in both *Daubentonia* and *Dactylopsila* and found similar specializations, including clinorhynchy, in both. Scott & Jepsen's (1936: pl. 5) side view of the skull of the Oligocene apatemyid *Sinclairella* suggests a certain degree of clinorhynchy but less than occurs in *Dactylopsila*. Skulls of *Heterohyus* are virtually unknown, but the incisors are robust and higher-crowned than in *Sinclairella* or *Dactylopsila*, although without the persistent pulps of *Daubentonia*. An arboreal mode of life hunting wood-boring insects is likewise envisaged for *Heterohyus*.

Paroxyclaenidae. Some similarities to the reduced bunodont to semi-bunodont cheek teeth of various viverrids (e.g. *Arctogalidea*) and procyonids (e.g. *Bassaricyon*, *Nasua*) are shown by the paroxyclaenid *Paroxyclaenus*. These viverrids and procyonids are mainly frugivorous and partly carnivorous (Walker 1975). Other paroxyclaenid genera (e.g. *Vulpavoides*, *Kopidodon*) have analogues in more insectivorous viverrids like *Bdeogale*, *Crossarchus* and *Eupleres*. Molar size reduction is accompanied by occasional increase in number in *Kopidodon* and also in the modern canid *Otocyon* (see Tobien 1969, Van Valen 1964). An approach to the semizalambdodonty of *Vulpavoides* is found in *Eupleres*, although here the teeth are excessively reduced in size and robusticity. No exact modern analogue has been found for the curious high-cusped M^1 of *Vulpavoides cooperi*. *Otocyon* eats insects, especially termites, but is also partly frugivorous and carnivorous; *Eupleres* catches adult and larval insects by digging and also eats small tetrapods (Walker 1975). It is possible that *Vulpavoides* combined insectivory, carnivory and frugivory in its diet in a similar way.

Perissodactyla. The nearest modern relative is obviously no guide to diet in the three Creechbarrow palaeothere genera. However, *Propalaeotherium messelense*, a very close relative of *P. parvulum*, is recorded from Messel with preserved gut contents consisting in one case of leaves of several dicotyledon families (Sturm 1978), and in another of *Vitis* (grape) seeds (Koenigswald & Schaarschmidt 1983). Of the leaves, species of the Lauraceae and Apocynaceae predominate, with Annonaceae or Symplocaceae, Myrtaceae, Juglandaceae and Moraceae as more minor constituents; of these, only the Annonaceae, Symplocaceae and ?Moraceae occur in the poorly-known flora of Bed A3 at Barton Cliff (penecontemporaneous with Creechbarrow). The closely related *Lophiotherium siderolithicum* shows trends in premolar molarization, perhaps towards a coarser diet, but may still have been folivorous-frugivorous.

Plagiolophus curtisi is the largest species in the fauna so far known and has the highest-crowned teeth. These show, however, only incipient trends in hypsodonty and their pattern has been described as selenolophodont. A herbivorous diet, coarser than for either of the other palaeotheres, is suggested. The occurrence of upper and lower jaws preserved together at two localities suggests perhaps powerful jaw muscles. This together with the massive parallel-orientated procumbent canines and robust cheek teeth, unlike other species of the genus, suggests that it may have had rooting habits. This species exceeds the size range for arboreal folivores (see Text-fig. 70C and Eisenberg 1978), and for this and family-wide osteological reasons all three palaeotheres were likely to have been ground dwellers.

The probability of larger herbivorous perissodactyls like *Palaeotherium* and *Lophiodon lautricense* (from penecontemporaneous records from Hengistbury and Barton – see p. 214) having

occurred at Creechbarrow is high. The latter's molar specializations resemble those of modern tapirs, which feed on leaves of aquatic and low-growing terrestrial plants, favouring the most abundant taxa (Walker 1975). Fischer (1964: 69–70) compared their mode of chewing with that of both tapirs and pigs. He then, however, stressed the differences from tapirs: e.g. absence of evidence for a proboscis, presence of conical incisors and larger canines in *Lophiodon*. He compared the postcranial skeleton with that of the extinct Pleistocene species of the rhinoceroses *Dicerorhinus* and *Coelodonta*.

Artiodactyla. Estimating way of life of this group from either nearest living relative or modern dental analogue is difficult. There are two relevant Messel skeletons, *Messelobunodon* and *Masillabune*, with gut contents. Those of the dichobunid *Messelobunodon schaeferi* were found to be undetermined fungi along with decayed leaves and it was concluded that it acquired the former by rooting on the forest floor (Richter 1981). *Hyperdichobune* sp. 1 (p. 376), as it is a dichobunid, may have had similar habits, but the molar mesostyle and larger metaconule and incipient P^4 molarization might point to frugivorous or folivorous tendencies.

The gut contents of the haplobunodontid *Masillabune* were found to be leaves (Tobien 1980). The probability that *Haplobunodon venatorum* was also highly folivorous is supported by its convergent dental similarities to *Propalaeotherium* aff. *parvulum*.

Mixtotherium and *Dacrytherium* belong in different families but are dentally rather similar, being low-crowned and strongly selenodont with strong molar and, in the case of *Mixtotherium*, P^4 mesostyles. The closest modern analogues seem to be the indriid primates *Propithecus* and *Indri*. Particular similarities are the configuration of the upper premolars and molars with prominent recurved parastyles, especially like *Mixtotherium*. The main difference is the weakness of the selenodonty in the lower molars and in the lingual cusps of the upper molars. Modern indriids are predominantly arboreal folivores (Kay & Hylander 1978) but the postcranial skeleton of *Mixtotherium* is unknown. That of anoplotheres is, however, typically artiodactyl and it is likely that both genera were ground-dwelling folivores.

Dichodon had higher-crowned selenodont teeth than *Dacrytherium* and was larger, but like *Mixtotherium* P4 was molariform. Its blade-like anterior dentition without diastema was like *Dacrytherium* but appears to have no modern analogue. Modern tragulids and small cervids have higher-crowned molars and different food-gathering apparatus, with incisiform canines and a marked diastema. Modern tragulids are both frugivorous and folivorous but have simpler, less selenodont molars than *Dichodon*. Molars of modern small deer (browsers) are more comparable in their degree of selenodonty and development of upper buccal and lower lingual stylar cusps. It is considered likely that *Dichodon* was primarily folivorous.

Similarities of the teeth of cebochoerids (*Cebochoerus* and *Acotherulum*) to cercopithecid primates misled Filhol (1877*b*) to suggest a relationship between these and suoid artiodactyls (cebochoerids were originally classified as pigs). Similarities in brachyodont bunodont dental pattern of the Creechbarrow cebochoerids to the dominantly frugivorous cercopithecid taxa are striking and suggest a similar diet for them. Once again, the postcranial skeleton is unknown but it is likely that they were ground-living like most other artiodactyls.

Conclusions

This probable community, which is rich in primates, arboreal species generally and species with frugivorous and folivorous diets, is typical of a forest environment, amongst available modern habitat types (see Davis 1962, Nesbit Evans *et al.* 1981). Non-mammal support for this environment is the high proportion of shade-demanding land gastropods (Preece 1980*a*). The number of mammal species (40 excluding bats) is close to that of a modern temperate forest (Davis 1962). However, in view of the likely incompleteness of the Creechbarrow record (see p. 438; and Wolff 1975), the postulated original number (nearly double that recorded) is closer to that of a modern tropical forest (Davis 1962). Buchardt (1978), Châteauneuf (1980), Collinson *et al.* (1981), Daley (1972*b*), Murray & Wright (1974) and Wolfe (1978, 1980) have nevertheless all pointed to a cooler than tropical climate in northern latitudes in the Eocene. The warmest temperatures are thought to occur in the earliest Lutetian or latest

Ypresian, decreasing to a Palaeogene minimum by the end of the Priabonian (≏ late Ludian–early Stampian). The temperatures postulated on isotopic evidence by Buchardt (1978) for the age under discussion fall within the modern forest climate called paratropical by Wolfe (1979). A number of the nearest living relatives and nearest dental analogues of the Creechbarrow mammal assemblage are confined to tropical forest. This probably reflects the results of reliction and retreat from increasing seasonality (Daley 1972*b*) rather than an original geographical and climatic restriction. It is concluded that the Creechbarrow mammal fauna probably inhabited a forest, existing under a paratropical climatic regime. The diversity of tarsioids and of ground-dwelling frugivores and folivores suggests an abundance of low-growing shrubs but without dense herbaceous undergrowth.

No flora is known from the Creechbarrow Limestone, presumably for preservational reasons, but its probable time equivalent the Barton Clay bed A3 at Barton Cliff has yielded some fruits and seeds (Chandler 1960). In terms of nearest living relatives this small flora is thought to include two coniferous trees, three aquatic or subaquatic herbs, three marginal aquatic herbs/shrubs, six shrubs/small trees, two probable lianes and several unknowns (see Chandler 1960, 1964). Unfortunately this is a low-diversity assemblage dominated by those plant organs most likely to survive transport into a marine depositional environment. It is probably not a true representation of the vegetation of the area (Chandler 1964; M. E. Collinson, personal communication 1982).

The spatial relationships of the presumed forest to the shallow lake depositional environment of the Creechbarrow Limestone is unknown. In view of the unsorted appearance of the mammal assemblage it is unlikely to have been far away.

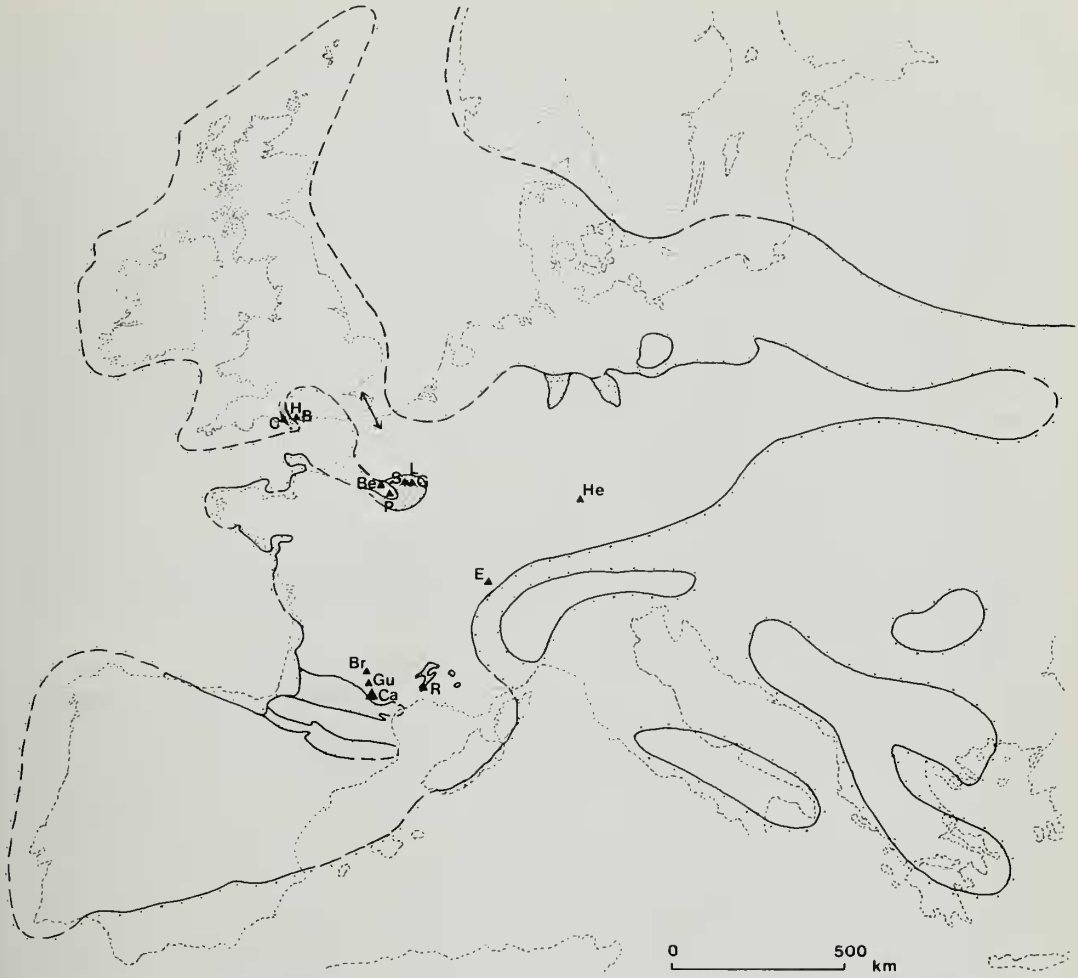
Palaeogeography

Faunal Provinces. Schmidt-Kittler & Vianey-Liaud (1975) and Schmidt-Kittler (1977*b*) divided the main European island area in the late Ludian into several faunal provinces based on rodents: 1, southern England plus Belgium and Germany west of the Rhine Graben; 2, southern Germany east of the Rhine Graben; 3, the Franco-Swiss area; and 4, Spain. At this time the inundated Rhine Graben (and possibly a non-marine area linking the latter to the Paris Basin, see Krutsch & Lotsch 1958) were important physical barriers. The former authors, however, considered that the main reasons for separation were ecological, a forested area existing in southern Germany east of the Rhine Graben, favouring such pseudosciurids as *Pseudosciurus* and *Suevosciurus*.

Franzen (1968: 158–159) distinguished northern and southern faunal provinces in the Ludian based on the genus *Palaeotherium*. His northern province equates with 1 and 2 of Schmidt-Kittler & Vianey-Liaud (1975) and his southern province with their 3 and 4. He noted a tendency for species with short, broad feet to occupy the north and for species with longer and more slender feet to occupy the south. He suggested that the north might have been a damper, more wooded region and the south drier and more open.

Sudre (1978*b*: 192–196) found some evidence from artiodactyls and primates to support Schmidt-Kittler & Vianey-Liaud's (1975) rodent provinces. He also noted endemic forms in the southern English Ludian (see also Sudre 1974), Spain and southern Germany.

Faunal provinces are less easy to envisage in the Bartonian because of the small number of localities, but there seems to be a tendency for endemics such as *Leptolophus*, *Plagiolophus cartailhaci*, *P.* aff. *annectens*, *Elfomys*, *Necrolemur*, *Peratherium*, *Saturninia*, *Adapis*, *Gliravus*, *Paradelomys*, *Pseudoltinomys*, *Anchilophus*, *Xiphodon*, and *Haplomeryx* to occur in the south. There is also a tendency for *Haplobunodon*, *Plagiolophus curtisi*, *Treposciurus*, *Suevosciurus*, *Nannopithex*, *Microchoerus* and *Scraeva* to occur in the north. An important zone of overlap occurs in the Mormont area of Switzerland. At the same time a number of taxa are widespread, e.g. *Lophiodon lautricense*, *Lophiotherium siderolithicum*, *Ailuravus stehlinschaubi* and *Plesiarctomys hurzeleri*. It seems that at least during some of the time there were no geographical barriers to dispersal in the later Bartonian. Evidence from southern Germany is restricted to one species (*L. lautricense*) from one locality (Heidenheim). Sediments of this age are sparse and



Text-figure 71 The palaeogeography of Europe in the Bartonian with *Lophiodon lautricense–Lophiotherium siderolithicum* Zone mammal localities. Fine dashed lines show outlines of modern land masses. Heavy lines show Bartonian coastlines, with dots on the seaward sides. Stipple indicates principal areas of non-marine sedimentation. Two-way arrow indicates position of postulated Weald–Artois land bridge. Abbreviations of localities: B = Barton; Be = Berville; Br = Le Bretou; C = Creechbarrow; Ca = Le Castrais localities; E = Eclépens-Gare and Eclépens A; G = Grisolles; Gu = La Guittardie; H = Hengistbury; He = Heidenheim; L = Latilly; P = Paris; R = Robiac; S = Sergy. Solid triangles indicate positions of localities. Sources of palaeogeographic data: Azzaroli (1981), Boccaletti & Manetti (1978), Krutsch & Lotsch (1958), Lemoine (1978), Ollivier-Pierre (1980), Plaziat (1981) and Pomerol (1973).

non-marine in the Rhine Graben (Sittler 1969) and it seems unlikely that it could then have formed a physical barrier to the spread of faunas from the north-west.

The English Bartonian mammals, except for the Barton and Creechbarrow endemics, must have reached the sites by means of an interchange with continental Europe. Heavy mineral evidence suggests that a land bridge from Dorset to the Cotentin peninsula existed in the Auversian (Morton 1982, i.e. top of his unit 7). It has also been suggested that the Weald–Artois Axis was active at this time (Pomerol 1973) and that a land bridge existed here between Britain and the continent during the later Bartonian. No direct evidence exists, owing to erosion of

Palaeogene sediments in the London Basin. Typical Barton Clay mollusc faunas, which might be expected to occur, are absent from Belgium to the east of the supposed bridge. The presence of continental European mammal species in the English later Bartonian strongly supports the presence of an at least intermittent Weald–Artois or Dorset–Cotentin land bridge. See Text-fig. 71 for palaeogeographic map of Europe in the Bartonian.

Migrations after the Bartonian. Schmidt-Kittler (1977*b*) thought that the primitive *Treposciurus* and *Suevosciurus*, being common to all provinces in the Ludian, may have represented 'relics of an earlier fauna common throughout Europe'. However, they are unknown in pre-Ludian deposits except at Creechbarrow. It is more likely therefore that they are differentiated in the northern area and intermittently spread southwards. *Treposciurus* was first, appearing in the early Ludian of Eclépens B, Fons 4 and Roc de Santa. *Suevosciurus* came later in the late Ludian of Entreroches and Escamps and the middle Oligocene of Armissan. Whether these genera were already in Bavaria before the Ludian is unclear. *Heterohyus morinionensis* may also have originated in the north and spread south, giving rise to *H. quercyi* of the French Ludian. *Leptadapis magnus* (including aff.) is not recorded from pre-Ludian strata except at Creechbarrow, but some lower molars from old Quercy collections with similar primitive morphology to those from Creechbarrow may be Bartonian.

Newcomers to the English early Ludian (for faunal lists, see Hooker & Insole, 1980) from the south are more numerous, e.g. *Isoptychus*, *Plagiolophus annectens*, *Pseudoloris parvulus*, *Quercygale angustidens*, *Gesneropithex* aff. *grisollensis*, *Gliravus*, *Catodontherium* and *Anchilophus*. English Ludian descendants of known English or northern endemic Bartonian taxa are restricted to *Scraeva* spp., *Treposciurus* spp., *Suevosciurus* sp. and *Microchoerus* spp., the list including genera that also spread southwards.

The mammalian fauna at the base of the Lower Headon Beds, including its newcomers of uncertain provenance, is thus very different from that which went before. It is dominated by semi-hypsodont theridomyids, palaeotheriids and artiodactyls, at the expense of the more brachyodont taxa, especially pseudosciurids, paramyids, lophiodontids, apatemyids and paroxyclaenids, which became either reduced in abundance and diversity or extinct. Certain little-modified surviving genera often show trends from frugivory towards folivory (e.g. *Microchoerus*).

This sudden faunal turnover is more likely to represent extinction and migration in relation to some important environmental change than an evolutionary jump. Such a turnover may be a critical point reaction to the more gradual floristic changes suggested by Collinson *et al.* (1981) in the Hampshire Basin coastal area in the late Eocene. Penecontemporaneous changes of a similar degree and nature occur in the mammalian faunas of southern France (Garimond *et al.* 1975), suggesting that the environmental change was on a European scale.

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